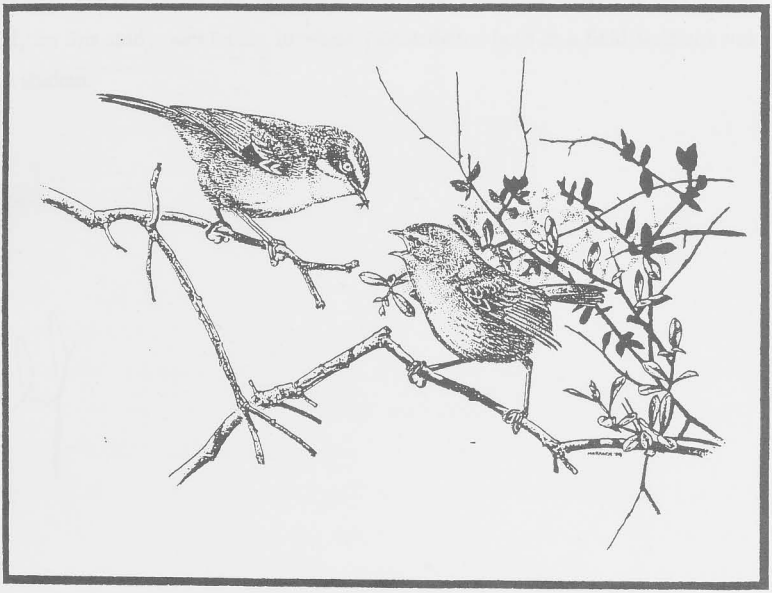
BROOD DIVISION AND POST-FLEDGING PARENTAL CARE IN THE WHITE-BROWED SCRUBWREN



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Declaration

The research described in this thesis is my own original research. Some of the data collected in the 1993 breeding season was used in partial fulfilment of the requirements towards my degree of Bachelor of Science with Honours. The vast majority of the data presented in this thesis, however, were collected as a postgraduate student during the 1996 and 1997 breeding seasons. Robert Magrath also generously shared his extensive data base collected during his extended study on this study population, to which I contributed both as a field assistant and as a student.

Signed

Ashley Leedman
October 2000

Acknowledgements

I dedicate this thesis to Shaanti Sekhon, who when I commenced this thesis was my friend, then my lover and is now my wife. She has been a tireless supporter of my work, both emotionally and, throughout the later stages, financially. Words cannot thank her enough.

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Finally, thanks to Peter Marsack, and those who commissioned him, for the wonderful drawing of the adult scrubwren feeding its offspring that graces the front of this thesis. It was an inspired wedding present and will forever remind me of what I saw down those binoculars for all those years.

GENERAL ABSTRACT

This thesis describes four aspects of post-fledging parental care in the white-browed scrubwren, *Sericornis frontalis*. First, it looks at the phenomenon of brood division. Second, it investigates the factors that control the length of nutritional independence. Third, it looks at factors that control the timing of natal dispersal and, fourth, it investigates how subordinate male help affected reproductive success and the proportion of care provided by the dominant pair. This study monitored 55 breeding attempts in the botanical gardens in Canberra, south-east Australia, over three breeding seasons, 1993, 1996 and 1997.

Brood division is the splitting of broods into discrete family units which are fed exclusively by one adult. There are many references to brood division in the literature, but there is good evidence for long term stable division for only a few species. Six functional hypotheses have been used to explain brood division. I tested these hypotheses and two novel hypotheses.

Brood division was the normal pattern of care for broods of two or three fledglings. Most of the functional hypotheses suggest that brood division is a parental strategy designed to maximise fledgling success. My results do not support this conclusion. Instead, I found evidence that brood division is a result of fledgling competition, and that adults did not display a strong preference for who they fed.

Adults and offspring are expected to disagree over the optimal length of parental care. In my study adults appeared to be in control of the length of care. Young from the same brood were fed for similar lengths of time. Further, aggression by adults towards young increased near the end of the dependency period, suggesting that adults were forcing young to become independent.

Young appeared to disperse of their own volition. Juvenile dispersal was bi-modal and peaked during the periods of low adult mortality, suggesting that they were dispersing into periods of favourable conditions. Young who dispersed late had the greatest chance of obtaining a breeding vacancy. No factor that I tested predicted why a male offspring might delay dispersal and remain on their natal territory beyond the beginning of the following breeding season.

Finally, females appeared to benefit more than alpha males from subordinate male help during the fledgling period. When subordinate males fed fledglings, the female reduced her proportion of care to young in both early and final broods for the season. The proportion of alpha male care, however, did not vary when beta males provided assistance. Although beta male help at the fledgling stage reduced the interval between reproductive attempts, it did not increase any measure of reproductive success and nor did it enhance female survival.

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CHAPTER ONE

INTRODUCTION

Parental care in altricial birds consists of four main periods: the incubation period, the nestling period, the period after young have left the nest but are still dependent on adults for food, and the period where young are nutritionally independent but remain on the territory (Skutch 1976). During the incubation period parental care consists mainly of keeping eggs warm, but adults must also protect the eggs against predation. During both the nestling and the post-fledging dependency periods, adults must also provision young at sufficient levels to promote optimal growth. Although adults no longer feed young during the final period, they may provide other aspects of care, such as protection from predators or teaching young how to best optimise their foraging techniques. Alternately, simply permitting young to remain on the territory while they develop necessary survival skills could be seen of as a form of parental care.

Most research into parental care in birds has focussed on the nestling period rather than the period between leaving the nest and leaving the natal territory, presumably because nests are easier to watch than mobile fledglings. This situation persists despite findings that the post-fledging period can be longer than the nestling period, parental feeding rates can be higher (Moreno 1984; Buitron 1988; McGowan & Woolfenden 1990; Evans-Ogden & Strutchbury 1997), and it represents a period of peak adult energy expenditure (Weathers and Sullivan 1989). Furthermore, post-fledging survival of young can markedly affect adult reproductive success (Clutton-Brock 1988, Weathers and Sullivan 1989).

My thesis will focus on several aspects of postfledgling care in the white-browed scrubwren, *Sericornis frontalis*. First, I will look at the pattern of food distribution between adults and their offspring, paying particular attention to the phenomenon of brood division. Brood division was the major focus of my research and field observations, and experiments were designed to test functional hypotheses. Second, I will look at factors that affect the variation in the length of post-fledging parental care among and within broods of scrubwrens. Third, I will look at the proximate causes leading to the timing of natal dispersal. In some species of birds some young remain on their natal territory during the following breeding season and may assist in provisioning young (Brown 1987). Since such cooperative breeding has been documented in the white-browed scrubwren

(Magrath and Whittingham 1997; Magrath and Yezerinac 1997; Whittingham *et al.* 1997; Whittingham & Dunn 1998; Magrath in press), I will also investigate what factors lead to natal philopatry. Lastly, I will investigate the effects of beta male help on reproductive success and the pattern of compensatory parental care. These areas encompass all aspects of the post-fledgling period and, although each alone forms a discrete area of research, combined they provide a complete view of the transition between leaving the nest and leaving home. The focus of this thesis is to explain why decisions are made and not to describe in detail how aspects of behaviour change over time. In particular, the emphasis is on describing the dynamic relationship between parents and their offspring where both act in order to maximise their own reproductive success, and understanding the set of behavioural rules which govern these processes.

Thesis Structure

This thesis will be laid out in seven different chapters. This chapter will introduce the four topics, the relevant literature and the underlying theoretical approach to each topic. The general methods section will include information on the study site and species and the general sampling protocol. It will also include general information on statistical methods common to two or more of the data chapters. The four data chapters will take the form of scientific papers. Each will have its own introduction, methods, results and discussion, although the introduction and methods will be abridged, as much of the information will be covered in the preceding chapters. Specific hypotheses and predictions will be developed in the introduction to each chapter. The final chapter will present general conclusions and deal with future directions.

Sibling Rivalry and Parent-offspring Conflict

Theoretical modelling suggests that parents and offspring will disagree about the level of care that young receive (Trivers 1974). Young are obviously more related to themselves than they are to either their siblings or their parents and

hence should behave in a way that maximises inclusive fitness, even if this is costly to others. Siblicide is an extreme example of young acting in a selfish way (Mock 1987). However, many less extreme forms of competition occur between family members and all stem from self-interest. Jostling by American robins, *Turdus migratorius,* for the best position within a nest is a good example (McRae *et al.* 1993). McRae *et al.* (1993) found that when adults fed from predictable locations on the nest, young competed with their siblings to obtain the best position. Further, broods which experienced brood reduction also experienced the highest levels of competition among nest mates to obtain the best position. However, as has also been predicted, some adults have evolved ways to counter these selfish demands (Parker and Macnair 1979). Crimson rosellas, *Platycercus elegans,* selectively feed young and females preferentially feed the smallest nestlings, except when food is insufficient for all chicks (Krebs & Magrath 2000). Rosellas feed young in a way that facilitates brood reduction when food is scarce, and yet minimises the risk of non-adaptive starvation of smallest young when food is not scarce.

Brood Division

In nearly all species of birds adults provide food to young after they have left the nest (Skutch 1976), although how they allocate that food has rarely been investigated. Of the few detailed studies of post-fledging care, some have revealed that individual adults of some species care for only a subset of the brood for all or a large part of the post-fledgling period (Horsfall 1984; Moreno 1984; McLaughlin & Montgomerie 1985; Edwards 1985; Harper 1985; Price & Gibbs 1987; Weatherhead & McRae 1990; reviewed in Table 1.1). In a brood of such species the female might care exclusively for one fledgling, for example, and the male may care for two; there are therefore two "subfamilies". It is unclear whether such "brood division" is the norm in birds, as has been suggested (McLaughlin & Montgomerie 1985), because there are too few detailed studies.

The function of brood division is unknown, although there are six main hypotheses. I now outline each hypothesis and suggest two more. These hypotheses and their predictions are summarised in Table 1.2.

(1) The Predation Hypothesis

Smith (1978) and McLaughlin & Montgomerie (1985) suggested that brood division reduces the risk of losing offspring to predators. Smith (1978) suggested that it may be possible for parents to remain closer to a small group of fledglings and so be better at warning them of the approach of danger while McLaughlin & Montgomerie (1985) suggested that if fledglings in divided broods are kept further apart than those in non-divided broods, then a predator finding one fledgling would not necessarily find and take the entire brood in a single attack. I suggest that it may be harder for a predator to find individual fledglings as opposed to large groups because they are potentially quieter in the absence of competition.

Regardless of the mechanism, the predation hypothesis suggests that brood division and separation should be most pronounced when young are most vulnerable, which in species such as yellow-eyed juncos, *Junco phaeonotus* (Sullivan 1989), and northern mockingbirds, *Mimus polyglottos* (Zaias & Breitwisch 1989), is soon after leaving the nest (however see Nilsson & Smith 1985). While the young of some species do separate and become "divided" immediately after fledging (e.g. song sparrows, *Melospiza melodia*, Smith 1978; Lapland lonspurs, *Calcarius lapponicus*, McLaughlin & Montgomerie 1985), other studies have shown broods remain together soon after fledging but divide as young become mobile (e.g., northern wheatears, *Oenanthe oenanthe,* Moreno 1984; European robins, *Erithacus rubecula*, Harper 1985; dunnocks, *Prunella modularis*, Byle 1990). The only study to directly test the predation hypothesis found no difference in predation rates between divided and non-divided broods of dunnocks (Byle 1990).

(2) Feeding Efficiency Hypothesis

Smith (1978) and Moreno (1984) suggested that brood division increases the rate at which young can be fed and/or decreases the amount of energy used by adults in feeding young. Adults with fewer young to care for will either be able to remain closer to those offspring and hence reduce travel time (Moreno 1984), or, as Smith (1978) suggested, be better able to remember their locations and thereby reduce time delivering. Moreno (1984) also suggested that adults might benefit by dividing the territory between them because they would then be better able to control depletion and renewal of food resources and have greater knowledge of patch profitability.

The idea that brood division should increase feeding rates has been directly tested in dunnocks (Byle 1990) and robins (Harper 1985), but both of these studies found that divided broods were not fed at a higher rate than undivided broods. However, brood division broke down in robins (Harper 1985) and in the medium ground finch, *Geospiza fortis,* and cactus finch, *G. scandens*, when food was superabundant (Price & Gibbs 1987), suggesting that brood division might have increased feeding efficiency.

Lapland longspurs provide indirect evidence that brood division might help increase feeding rates or reduce travel times (McLaughlin and Montgomerie 1985 & 1989). Lonspurs breed in a patchy environment and are subsequently able to reduce travel times by moving offspring to feeding patches. Furthermore, it benefits longspurs to separate brood members into smaller units because the whole brood together would deplete a patch quicker and hence necessitate more frequent moves. Therefore, brood division in the longspur decreases travel time and hence might decrease parental energy expenditure and/or increase the rate at which young are fed.

(3) Sibling Competition Hypothesis

Brood division might enable the equitable distribution of food to young by reducing the effects of sibling competition (Smith 1978; Harper 1985). This may occur through two mechanisms. First, Smith (1978) suggested that sibling competition may be reduced in smaller groups of young and eliminated if there is

a single fledgling in the subgroup. This hypothesis predicts that food will be allocated more inequitably as the number of young in the sub-group increases, leading to greater differences in condition between the biggest and smallest offspring.

Second, if an adult of a divided sub-family has perfect knowledge of the amount of food that each fledgling has received, because no other adult feeds "their" young, they may be less susceptible to manipulation by exaggerated begging calls (Harper 1985). Research on nestlings has shown that an increase in the level of begging can result in an increase in the amount of food provided by the adult (e.g., Bengtsson & Ryden 1983) which presumably occurs because the adult perceives that offspring to be hungry and is also uncertain about the total amount of food that the individual has received. In theory, the fledgling can manipulate the adult's uncertainty into providing it with more food. Brood division, therefore, could be a counter-strategy by adults to maintain perfect knowledge and hence be able to ignore exaggerated signals.

The only study to directly test the hypothesis that brood division reduces the inequality in weight between offspring was Harper (1985), who looked for and failed to find a difference between young from divided and non-divided broods of robins. Like the feeding efficiency hypothesis, this hypothesis also predicts that brood division should break down under conditions of super-abundant food (as found by Harper 1985 and Price & Gibbs 1987), as the need to distribute food evenly is reduced. No study has tested the hypothesis that brood division is a counter-strategy to exaggerated begging calls.

(4) Division by Sex Hypothesis

There may be an advantage for a particular sex of adult to feed a particular sex of offspring (Horsfall 1984; McLaughlin & Montgomerie 1985). Three such advantages have been suggested. First, if one sex of adult feeds more than the other, then there may be an advantage for that adult to feed a particular sex of offspring, perhaps the more dispersive sex (Horsfall 1984; McLaughlin & Montgomerie 1985). Second, if adults displayed an inter-sexual foraging difference then it would be beneficial for young to be cared for by an adult of the same sex (McLaughlin & Montgomerie 1985) and third, increased exposure of

young to family members of the opposite sex might facilitate mate choice later in life (McLaughlin & Montgomerie 1985).

An association between adult and offspring sex has been suggested to occur in three species, but sample sizes were small or young were sexed indirectly. In two species, adults tended to care for young of the same sex while in the other species adults cared for young of the opposite sex. In robins, males tended to care for larger fledglings, and male fledglings are on average larger than females (Harper 1985), however it is unclear whether division is based on sex or size. In dunnocks, adults tended to care for offspring of the same sex (Byle 1990), but sample size was limited to 10 individuals. In blackbirds, *Turdus merula,* adults cared for young of the opposite sex (Snow 1958), but the sample size consisted of only three male and one female offspring.

None of the above studies that found an association between adult and fledgling sex suggested that the relationship found explained the occurrence of brood division. Harper (1985) suggested that the relationship between the sex of the adult and the sex of the fledgling might explain how adults selected which young to feed but not why brood division occurred as, in his study, not all broods divided. Byle (1990) made a similar observation and commented that it would be difficult to see how division by sex would be advantageous as several broods in his study also did not divide. Studies on bluethroats, *Luscinia svecica,* (Anthonisen *et al.* 1997) and hooded warblers, *Wilsonia citrina,* (Evans Ogden & Stutchbury 1997) have looked for a relationship between the sexes but have not found one. A problem until recently was that young birds could not be sexed, but this has been solved with the development of molecular techniques (Griffiths *et al.* 1998).

(5) Sexual Conflict Hypothesis

Males or females might attempt to choose the young requiring the least post-fledging care (Slagsvold *et al.* 1994). Young may be chosen by sex or by size. There is currently no evidence to suggest that different sexed young require different amounts of parental care but few studies have looked at this question. The size of the offspring may affect the amount of food it requires postfledging, but it is not intuitive as to which direction this might go. Larger fledglings may

require less care because they mature faster or, alternately, more care because they require more food.

Slagsvold *et al.* (1994) found indirect evidence that in blue tits, *Parus caeruleus*, larger fledglings required less care. After manipulating hatching spread, which increased the weight difference between largest and smallest young, he found that males cared more often for larger fledglings and, subsequently, increased their survival to the next breeding season at the expense of the female. No other study has tested this hypothesis.

(6) The Adult Manipulation Hypothesis

Brood division might be an adult strategy to enforce 'even' levels of care by all adults within the group (Magrath pers. comm.). If an adult feeds one or more fledglings, but refuses to feed others, it places the other adults in the position of forcing them to provide adequate care for the remaining fledglings, or letting them die. This hypothesis is analogous to the game theory model which predicts stable bi-parental care of young only if adults respond to another's reduction in care by reducing their own effort by a smaller amount (Houston & Davies 1985). However, that game theory model requires that adults can monitor the provisioning rates of others, whereas this hypothesis does not. Monitoring feeding rates of other adults may be difficult or impossible during the fledgling stage as fledglings can be found anywhere on the territory, compared with nestlings which are fed at a specific place. Therefore, brood division might be a strategy which enforces stable bi-parental care in an environment where adults cannot easily monitor another adult's feeding rate.

(7) Fledgling Choice Hypothesis

In contrast to the preceding hypotheses, brood division might be the outcome of choices made by the young, not by the adults. Fledglings may follow a particular adult, perhaps excluding others. This may result in the most dominant fledgling being associated with the best feeder.

Slagsvold (1997) first suggested this idea in response to findings that largest chicks were often fed by the adult who provided the most food, as in

American robins (Weatherhead & McRae 1990). However, he qualified this idea by suggesting that it did not provide an ultimate explanation of brood division, but rather predicted which chick would be associated with which adult. I go further and suggest that the fledgling choice hypothesis might be an ultimate explanation of brood division and that adults might have no preference as to which young they feed.

(8) Adult Dispersion Hypothesis

I suggest that brood division may be non-adaptive and simply a result of a break-down in the adult pair bond after young have left the nest. If adults feed in separate parts of the territory or do not remain territorial after young have left the nest, then a young might be forced to choose an adult and remain with that adult for the rest of its dependency period because there is simply no opportunity to swap between feeding groups. Brood division might, therefore, be a result of parental separation without being the cause of parental separation.

Brood division has been associated with parental separation in northern wheatears (Moreno 1984), Lapland longspurs (McLaughlin & Montgomerie 1985 & 1989), hooded warblers (Evens Ogden & Stutchbury 1996) and bluethroats (Anthonisen 1997). In bluethroats, males and females often fed their fledglings away from each other. While males mostly remain on their nesting territory, females will move some considerable distance away, up to 650 metres. In circumstances such as these, it would be very difficult for a fledgling to switch adults. It should be noted however, that brood division still occurs in species such as American robins (Weatherhead & McRae 1990) which do not divide their territory and where the fledglings were found together in over 20% of observations, indicating that, in some species at least, dispersion is not enough to fully explain division.

Problems in Understanding Brood Division

Progress in documenting brood division and understanding its function has been hampered by careless use of the term "brood division" and associated inappropriate sampling protocols. The term should be reserved for broods divided into sub-families for a substantial period of post-fledging care, with each sub-family consisting of specific adults and young. In contrast to brood division, it may be inevitable that adults will have short-term biases in feeding young that are closer or of known locations. For example, McGowan and Woolfenden (1990) found that although a fledgling scrubjay, *Aphelocoma coerulescens,* was in some cases fed exclusively by an adult within an observation period of two hours, it was not fed preferentially by the same adult during subsequent observations. The authors argued, correctly, that this was not brood division. It follows that "brood division" cannot be shown by observations taken on one or a few days. This is true even if there are many feeds per day, because such data are non-independent in the context of the post-fledging period as a whole. Unfortunately, all studies of brood division include at least some non-independent data, although some do include observations from several days for at least some young (Table 1.1).

Developing a theoretical framework for understanding brood division, and assessing the function of brood division, is also hampered by incorrectly equating short-term feeding biases with "brood division". Several hypotheses supposedly addressing the issue of "brood division" only suggest a benefit of keeping young separate, or perhaps explain why there might be short-term biases, but do not explain why the same adults should care for the same fledglings for many days. For example, adults need only keep young apart to reduce depredation of offspring, they do not need to exclusively feed separate young. The same applies to both the feeding efficiency and the sibling competition hypotheses; young need to be fed in separate sub-families but sub-families do not need to be preferentially fed by the same adult every day. Adults could feed one group one day and another group the next. The choice by sex and the sexual conflict hypotheses predict long term division as they are based on features which do not change over the duration of dependency. The fledgling choice hypothesis, however, is based on size and dominance, both of which can, theoretically, change but are, perhaps, unlikely to. If the largest fledgling chooses the adult that provides the most food

then it is likely to remain the largest fledgling throughout its period of dependency and brood division will remain stable. The adult manipulation hypothesis also predicts long term division. If adults switched young between them, then one adult could feed less, forcing the other to compensate when it fed. The parental separation hypothesis predicts that division will remain stable as long as adults remain a sufficient distance apart. These issues will be dealt with in more detail in the chapter on brood division.

The Duration of Fledgling Dependency

Although many studies have documented the duration of parental care for birds after young have left the nest (e.g., Moreno 1984; Buitron 1988; McGowan & Woolfenden 1990; Yoerg 1998; Magrath *et al.* 2000), few have investigated why it varies between individuals within the same breeding population (Nilsson & Smith 1985; Yoerg 1998). Variation in duration of dependency between individual offspring could result from several factors. For example, large fledglings may voluntarily terminate parental care in order to disperse earlier (Nilsson & Smith 1985; Bustamante 1994). Alternately, fledglings may have no control over the length of their care and adults may stop feeding them at a time that is advantageous to them but not optimal for their offspring. This is particularly likely when adults renest or have to prepare for winter (Weathers & Sullivan 1989; Leonard *et al.* 1990; Svensson & Nilsson 1997).

Parent-offspring conflict theory provides a framework for investigating the variation in dependency times. Trivers (1974) suggested that offspring will demand more food from adults than they are prepared to provide, as they care more about themselves than they do about their parents. Conflict theory also predicts that adults will evolve ways of countering these elevated demands (Parker & Macnair 1979; Stamps *et al.* 1985). One way fledglings could manipulate their feeding levels is by manipulating adults to extend their period of nutritional dependency. This may be optimal for the fledglings long term reproductive success but sub-optimal for the adults. Adults, of course, may counter these selfish demands, the simplest methods being to stop feeding

(Weathers & Sullivan 1989) or to attack their offspring (Alonso *et al.* 1987; Leonard *et al.* 1990). Two hypotheses have been proposed to explain the proximate causes leading to the termination of parental care, these are the trade-off hypothesis and the parental termination hypothesis.

(1) The Trade-off Hypothesis

The trade-off hypothesis suggests that the termination of parental care is the result of an interaction between the increased ability of the offspring to obtain food through self-foraging and an increased reluctance of adults to provide food to the offspring. Figure 1.1a provides a graphical presentation of this hypothesis. Immediately after leaving the nest, fledglings are unable to forage and so must obtain all food from their parents. As young age, their foraging ability improves and their parents become increasingly reluctant to provide food. After point *p1* in Fig.1.1a, offspring obtain more food by self-foraging than they do by begging and so switch foraging strategies. Young spotted flycatchers, *Muscicapa striata*, for example, became independent when the returns from self-foraging were greater than those of begging for food (Davies 1976). This model, of course, over-simplifies the process of the transition to independence. Before reaching the point *p1* young may practice self-foraging, perhaps when satiated or left alone, in order to improve their foraging ability. Figure 1.1a also assumes that begging and self-foraging are mutually exclusive, hence the sudden shift after point *p1* to self-foraging.

In species such as the white-whinged chough, *Corcorax melanorhamphos*, the transition to self-foraging occurs more gradually. Choughs have a very long period of dependency, about 200 days, and the transition to complete dependence is characterised by a gradual improvement in foraging ability and a gradual decline in returns from begging (Heinsohn 1991). White-winged choughs, therefore, become fully independent at the point where the begging curve joins the X axis in Fig. 1.1a, but pursue a mixed strategy of self-foraging and begging for food after point *p1*, when self-foraging is on average more productive. The difference between choughs and spotted flycatchers may be to do with their foraging techniques. Flycatchers take most of their prey on the wing and it may be difficult for juveniles to both forage for themselves and beg from adults and so

they become independent when their returns are maximised by concentrating solely on self foraging. Choughs, however, forage on the ground and in large groups. It would, therefore, be possible for juveniles to alternate between self-foraging and begging, particularly if they were able to observe adults about to find food and then devote energy to begging before the adult could consume its prey item.

Regardless of whether the transition to independence occurs suddenly, as in the flycatcher (Davies 1976) or more gradually, as in the white-winged chough (Heinsohn 1991), the trade-off hypothesis predicts that some characteristic of individual offspring, such as size or foraging ability, will affect their length of care.

(2) The parental termination hypothesis

The second hypothesis suggests that adults alone are in control of the length of juvenile dependency and terminate care at a time when begging is still more profitable than self-feeding for young. Weathers and Sullivan (1989) found that feeding fledged offspring was the most energetically expensive time of the breeding cycle for adults and, as such, adults are likely to try and minimise the length of this period (see also Drent & Daan 1980). Figure 1.1b displays this concept graphically. Instead of a gradual decline in parental willingness to feed, adults suddenly terminate feeding at a time which is to their advantage, *f1*, but before young would choose. Immediately after this period young should experience a drop in food intake. Parent-offspring conflict theory predicts this outcome. Fledglings could be expected to demand more food from adults or demand food for longer than adults are prepared to give, which would result in adults making a decision as to how long they will feed for and then stopping.

Evidence for the parental termination hypothesis comes from several species. For example, in imperial eagles, *Aquila heliaca* (Alonso *et al.* 1987), adults gradually reduce the amount of food they provide to offspring while offspring demands increase. Finally, adults terminate care and are aggressive towards offspring, initially forcing dependency and then dispersal. In the black-capped chickadee, *Parus atricapillus*, adults also use aggression to discourage young from begging and following them about the territory (Leonard *et al.* 1990).

Further evidence that adults terminate care before the offspring choose to do so also exists for the yellow-eyed junco, where 42% of offspring perished in the first two weeks after the forced termination of parental feeding (Weathers & Sullivan 1989).

Adults should terminate care to offspring if it increases the adults' future reproductive success. One such method of increasing reproductive success is to increase the number of breeding attempts per season (Evens Ogden & Stutchbury 1996). Adults may achieve this by terminating care to early broods in order to rapidly renest (Weathers & Sullivan 1989). Indirect evidence for this occurs in two species, blackbirds (Edwards 1985) and great tits, *Parus major*, (Verhulst *et al.* 1997). In these species, adults devote more care to second broods than they do to first broods. Early in the season adults maximise their reproductive success by reducing care to current offspring in order to renest, while late in the season adults maximise their success by extending care to their current offspring because they no longer have reproductive alternatives. This finding has been experimentally confirmed in great tits (Verhulst *et al* 1997), where the removal of second broods resulted in an increase in the length of care for first broods.

Adults may also terminate care if it compromises their future survival. One way care to offspring may compromise survival is if it affects their moult date. For example, adult hooded warblers that had second broods delayed moult by up to three weeks (Evens Ogden & Stutchbury 1996). A delay in moult date may be costly for migratory species if it delays their arrival on winter foraging grounds (Evens Ogden & Stutchbury 1996). In non-migratory birds, a delay may compromise their over-winter survival by reducing the amount of fat reserves they can obtain before the onset of cold weather (Svensson & Nilsson 1997). In circumstances such as these, it may be more profitable for adults to terminate care at some cost to offspring than to extend care and compromise their own survival. In coots, *Fulica atra*, adults fed young less late in the season, perhaps because feeding young reduced their ability to moult (Amat 1995).

Distinguishing between hypotheses

Distinguishing between the trade-off and the parental termination hypotheses is conceptually easy. In the trade-off hypothesis, the date of dependence is

negotiated by adults and offspring. In this hypothesis, fledglings can extend the duration of care by manipulating the adults into providing more food than is optimal, while the adults can reduce the length of care by controlling the returns from begging and, hence, forcing independence. In the parental termination hypothesis, however, adults are in complete control. In practice it is difficult to predict how the two hypotheses will differ as both predict that individual characteristics will be important. In the trade-off hypothesis, different young will have different levels of return from begging and self foraging (Heinsohn 1991), while in the parental termination hypothesis, adults may value young differently and adjust their levels of care accordingly. The real difference in the hypotheses lie in the shape of the adult feeding curve (Fig. 1.1a & 1.1b). In the trade-off hypothesis (Fig. 1.1a), the returns from begging gradually diminish, particularly when young pursue a mixed strategy of alternate begging and self-foraging, while in the termination hypothesis (Fig. 1.1b), the returns from begging end abruptly. Further difficulties arise in distinguishing between these hypotheses because parental feeding rates may drop suddenly in situations where adults terminate care and at the time when young stop seeking food because they can obtain greater returns from self-foraging. If parental care terminates suddenly because adults have stopped feeding before young have stopped begging, then the end of care should be accompanied by either parental aggression or adults refusing to feed begging young.

Further, there may be no conflict over the length of juvenile care in some species. Nilsson and Smith (1985) found that large marsh tit, *Parus palustris*, young became independent earlier than their smaller siblings and suggested that this occurred because it allowed for earlier dispersal which increased the offspring's chances of gaining a breeding vacancy. Black kites, *Milvus migrans*, are another species where there appears to be little conflict over the date of nutritional independence (Bustamante & Hiraldo 1990). In this species, the end of parental care coincides with the beginning of migration. Further, some young dispersed from their natal territory before adults had stopped providing food, indicating that the need to migrate was more important than the benefit of extended parental care. In species such as marsh tits and black kites, where the length of nutritional independence is closely tied to the length of natal philopatry, there may be no conflict of interest between adults and offspring over length of

dependency, as both maximise their reproductive success by minimising the time that young are cared for.

The Timing of Natal Dispersal

After becoming nutritionally independent, young of most species face the decision of when to leave their natal territory. Little is known about what factors determine this date or to what extent characteristics of individuals affect its variation. In some species, such as marsh tits (Nilsson & Smith 1985) and yellow-eyed juncos (Weathers & Sullivan 1989), natal dispersal occurs soon after young become independent. Marsh tits leave home as soon as they are able to forage for themselves as this provides them with the best opportunity of finding a breeding vacancy. But in species such as white-winged choughs (Heinsohn 1991), white-throated magpie jays, *Calocitta formosa* (Langen 1996), and fairy wrens, *Malurus cyaneus* (Mulder 1995), natal dispersal does not coincide with the termination of parental care. Young, if they do leave their natal territory, may remain at home for weeks or months after the termination of parental feeding. Although there is an extensive body of literature on why young might delay dispersal (see reviews by Wiley & Rabenhold 1984; Brown 1987; Koenig *et al.* 1992; Emlen 1995) or how far they should disperse (Greenwood & Harvey 1982; Weatherhead & Forbes 1994; Paradis *et al.* 1998), there is little information on the factors that affect the variation in the timing of dispersal among individual offspring.

In my thesis I will focus on the proximate factors that affect the variation in the timing of dispersal of birds that leave their natal territory. I will not focus on the more complex problem of what causes delayed dispersal and which individuals leave. In species in which some but not all young leave, offspring must first decide if they will leave and then decide when. These questions are beyond the scope of my research as they involve issues apart from parental care and fledgling development.

Two possible scenarios have been used to explain the proximate factors leading to natal dispersal. First, young leave at a time which maximises their

chances of survival, finding a mate or gaining a breeding vacancy (Nilsson & Smith 1989, Nilsson 1990, Kenward *et al.* 1993, Mulder 1995). Second, young are forced to leave their natal territory by their parents (Weathers & Sullivan 1989) or siblings (Kinnaird & Grant 1982; Black & Owen 1989; Strickland 1991), and at a time when their reproductive success is compromised. The former hypothesis suggests young choose when to leave home and the latter suggests they are forced out.

(1) Voluntary dispersal

If dispersal is voluntary then presence or absence of adults on the territory should not affect dispersal dates (Nilsson 1990). To test this hypothesis, Nilsson (1990) removed adult marsh tits who were feeding offspring and replaced them with supplementary food stations. Young still dispersed. He concluded that parental aggression was not the proximate cause of dispersal. In marsh tits, males who disperse early are most likely to find a breeding vacancy (Nilsson 1989). Therefore, minimising the dependency period of offspring is optimal for both adults and offspring and there is no conflict of interest. Similar results were found in goshawks, *Accipiter gentilis*. Kenward *et al.* (1993) provided supplementary food to goshawks with dependent young and in a number of cases also removed the adults. They found that young from both groups dispersed at roughly the same age, again suggesting that some factor other than parental aggression was forcing dispersal. Kenward *et al.* suggested that young goshawks were dispersing into a period where young rabbits, their main food source, were plentiful. Dispersing into conditions of high food abundance may be easier because young could hone their foraging skills while searching for breeding opportunities without having to worry about starvation.

Brown (1987) suggested that dispersal might be delayed in some species because offspring need to remain with parents until they have acquired the necessary skills for successful dispersal and independent breeding. This hypothesis was tested by Langen (1996) in magpie-jays. Male magpie-jays showed great variation in the age at which they dispersed, with birds leaving between 4 and 23 months after leaving the nest. Males dispersed earlier from larger groups and they generally dispersed at the beginning of the breeding

season. Dispersal, in this case, was a result of males optimising their chances of gaining a breeding vacancy and not because they needed to acquire skills. Instead of acquiring certain skills, young might be constrained by needing to reach a critical body mass before being able to disperse. Female fairy-wrens have a bimodal dispersal pattern: those born early in the season tend to disperse within that breeding season while those born later delay dispersal until the beginning of the next breeding season (Mulder 1985). One explanation of this behaviour is that early hatched young are able to obtain enough body reserves to attempt dispersal while those hatched later must wait until the following spring. However, this pattern is flexible. In one brood a female dispersed early while her sister remained until the beginning of the following breeding season.

Characteristics of individual offspring may also affect when they leave their natal territory. Indeed, the great variation in dispersal dates from within the same breeding population and from within the same brood (Mulder 1985; Langen 1996) strongly suggests that individuals may have different optimal dispersal dates. In Nilsson and Smith's (1985) study, large great tit offspring dispersed earlier than small ones. Smaller birds, they suggested, needed to remain on the territory longer in order to acquire the necessary skills needed to survive after dispersal.

Sex might also affect dispersal date. This is obviously true for species where one sex remains philopatric. But in species where both sexes disperse there may be an optimal time for each sex. Female goshawks dispersed later than male goshawks but no explanation was provided for this behaviour (Kenward *et al.* 1993). Perhaps males matured quicker or disproportionately increased their chances of finding a breeding vacancy by dispersing earlier.

(2) Forced Dispersal

Young may be forced from their natal territory rather than leaving voluntarily (Strickland 1991; Winker *et al.* 1995). For example, aggression is closely related to the disappearance of young from family flocks of barnacle geese, *Branta leucopsis* (Black & Owen 1989). In this species, aggression is directed both by the dominant adults and the dominant siblings towards less dominant young. It is to the advantage of adults and dominant siblings to expel less dominant members

of the group as being in a large family group can be costly, because the foraging patch is depleted at a greater rate. In this example both mechanisms are important. Larger birds choose their optimal dispersal time while their smaller siblings are forced to disperse before they would normally choose to do so. Another example of forced dispersal comes from superb fairy-wrens. Females who remained in the group until the beginning of the next breeding season were forcibly expelled by the dominant female (Mulder 1995). Interestingly, female young that dispersed in the breeding season in which they were born apparently left of their own volition as no aggression was seen during that stage.

The Effect of Helpers on Fledgling Survival and Parental Effort

A small percentage of birds breed with the assistance of extra-pair helpers (Brown 1987). Two main benefits are commonly cited for such cooperative breeding. One, that it increases offspring survival (Hatchwell & Davies 1990; Emlen & Wrege 1991; Komdeur 1994) and two, that it allows one or both of the breeding adults to reduce their work rate (Stallcup & Woolfenden 1978; Russell & Rowley 1988). Most studies that have documented increases in survival or decreases to parental work rates have done so at the nestling stage, despite the fact that parental feeding rates and parental effort can be greater during the fledgling stage.

Benefits of help

Individuals in the dominant pair have two choices when receiving assistance from helpers; either they can maintain their unassisted level of feeding, in which case the extra help becomes additive, or they can reduce their level of provisioning to the point where the offspring receive the same amount of food as they would when fed by a pair alone (Hatchwell 1999). Examples exist for both situations. In white-fronted bee-eaters, *Merops bullockoides*, parents maintain the same level of care regardless of the number of helpers so that more helpers result in more food to the offspring and a corresponding increase in survival (Emlen & Wrege

1991). White-winged choughs are another species where extra help increases offspring survival. In this species, the dominant pair is unable to produce offspring alone and requires several helpers to achieve success (Heinsohn 1992). In other species, such as the superb fairy wren, the presence of helpers does not increase total feeding rates but does reduce the amount of food provided by the dominant pair, with net result being that reproductive success remains the same (Dunn *et al.* 1995).

When should adults reduce care?

In trying to understand why helping behaviour varies between species, Hatchwell (1999) suggested extra help should be additive where nestling starvation is high and compensatory when starvation is low. In a review of 27 cooperatively breeding species, Hatchwell found general support for both predictions; that is, where nestling starvation was high, help was generally additive and reproductive success increased, and where starvation was rare, help was compensated for by a reduction in provisioning by the dominant pair and there was no effect on reproductive success. He did not, however, find that the survival of the dominant pair increased in those species in which they showed a compensatory response to the presence of helpers. Other studies, however, have found that breeder survival does increase with extra help, but these studies do not differentiate between the effects of reduced work rates or group size per se (Stallcup & Woolfenden 1978; Sherley 1990). For example, in splendid fairy-wrens, *Malurus splendens*, 76% of females who bred with helpers survived until the next breeding season whereas only 55% without helpers survived, but no mention is made of the effect of helpers on parental feeding rates (Russell & Rowley 1988). Rifleman, *Acanthisitta chloris*, are another species where help appears to increase female survival. Paradoxically, in this species female effort is not reduced but survival is, while male effort is decreased but survival is not (Sherley 1990). No study that I am aware of shows a direct relationship between the feeding rates of helpers and parental survival.

Why Do Males and Females Sometimes Differ in their Response to Helpers?

Hatchwell (1999) noted that males and females did not respond in the same manner to the presence of extra help. The differences between the sexes were manifest in two ways. First, he found that the relationship between a compensatory reduction in care and low nestling starvation was stronger in females. Second, he found that males tended to exhibit compensatory reduction in care when their survival was low, whereas females only reduced care when starvation was uncommon. He suggested that males were more concerned about their own survival and females were more concerned about the survival of the brood. A possible explanation of this result is that males are less certain of their paternity than are females and so are more likely to reduce care, particularly when there are other birds to compensate for their behaviour.

An example of a reduction of care by males when paternity is uncertain occurs in the dunnock, where the level of parental care in either the alpha or beta male varies with the amount of time that each spent with the female during her fertile period (Davies *et al.* 1992). Alpine accentors, *Prunella collaris*, are another species where male care has been shown to vary depending on their level of paternity, although in this species only the alpha male is sensitive to variance in paternity. This is most likely because alpha males had opportunities to obtain future matings with other females while the beta did not (Hartley *et al.* 1995).

Why do some studies show no benefits of extra help?

In some species, no convincing link has been found between extra help and either a reduction in parental effort or an increase in reproductive success. In groups of white-browed scrubwrens with older breeding females, helpers increased the total amount of food provided to the nest but there was no effect on reproductive success (Magrath & Yezerinac 1997). Furthermore, there was no evidence that subordinate male help increased the survival of the dominant pair. However, in groups with yearling females, cooperative breeding did increase reproductive success (Magrath in press). Unfortunately, the data so far present an incomplete picture of subordinate male care because care of fledglings has not been studied.

Aims of Thesis

The primary aim of this thesis is to investigate the functional hypotheses which attempt to explain brood division. Brood division is a recurring theme in many studies which focus on the fledgling period, but no study has provided a convincing explanation for this behaviour. Furthermore, despite the number of studies which discuss this phenomenon, the underlying theory is still poorly developed and contains conceptual flaws which hinder our understanding. I will also investigate factors that determine the length of parental care and of natal philopatry, and attempt to understand the variation between individuals, both within and between broods. Finally, I aim to investigate how the proportion of care provided by the dominant pair changes when the breeding attempt is assisted by an extra male.

The overall aim of this thesis is to increase understanding of the fledgling period as a whole, particularly the decision rules of both adults and fledglings. Very few studies have looked at this period in detail, and of those that have, fewer still have looked at the reasons why some offspring behave differently from others, particularly from their siblings. Understanding this variation will help us understand the rules used by both adults and their young when 'deciding' such things as who feeds whom, how long offspring should be fed, when they should leave home and, in the case of cooperative families, how much each adult should contribute to the care of young.

Table 1.1. Reports of brood division. Observations are considered to be independent if separated by at least two hours. The number of broods divided is broken into E, early broods and, F final broods. Where the nest order is not given it is because the order was either not given in the reference or the species only produced one brood per season.

Species	Family*	No. of divided broods	Author
A. At least six independent observations on marked individuals			
Eurasian Coot *(Fulica atra)*	Rallidae	2/3	Horsfall 1984
Robin *(Erithacus rubecula)*	Muscicapidae	1/5 E 4/5 F	Harper 1985
American Robin *(Turdus migratorius)*	Muscicapidae	5/11	Weatherhead & McRae 1990
Eurasian Blackbird *(Turdus merula)*	Muscicapidae	8/43 E 44/44 F	Edwards 1985
Cactus Finch *(Geospiza scandens)*	Fringillidae	3/3	Price & Gibbs 1987

Cont.

Species	Family*	No. of divided broods	Author
B. Between 2-5 independent observations on marked individuals			
Wheatears (*Oenanthe oenanthe*)	Muscicapidae	7/7	Moreno 1994
Northern mockingbird *(Mimus polyglottos)*	Sturnidae	0/36 E 4/11 F	Zaias & Breitwisch 1989
Dunnock (*Prunella modularis*)	Passeridae	12/22	Byle 1990
Lapland Longspur *(Calcarius lapponicus)*	Fringillidae	10/10	McLaughlin & Montgomerie 1985
C. Between 1-2 independent observations on marked individuals			
Bluethroat (*Luscinia svecica*)	Muscicapidae	4/5	Anthonisen *et al.* 1997
Song Sparrow *(Melospiza melodia)*	Fringillidae	53/68	Smith 1978

Cont.

Species	Family*	No. of divided broods	Author
D. Reference to brood splitting			
Hairy Woodpecker *(Picoides villosus)*	Picidae		Kilham 1968
Red-bellied Woodpecker *(Melanerpes carolinus)*	Picidae		Kilham 1961
Common Crane *(Grus grus)*	Gruidae		Cramp & Simmons 1980
Redknobbed Coot *(Fulica cristata)*	Rallidae		Dean 1980
American Coot *(Fulica americana)*	Rallidae		Harrison 1978; Lyon *et al.* 1994
Hudsonian Godwit *(Limosa haemastica)*	Scolopacidae		Harrison 1978
Bar-tailed Godwit (*Limosa lapponica)*	Scolopacidae		Harrison 1978
Marbled Godwit *(Limosa fedoa)*	Scolopacidae		Harrison 1978
Whimbrel *(Numenius phaeopus)*	Scolopacidae		Williamson 1946
Common Snipe *(Gallinago gallinago)*	Scolopacidae		Tuck 1972
Golden Plover *(Pluvialis apricaria)*	Charadriidae		Williamson 1948
South Polar Skua *(Stercorarius maccormicki)*	Laridae		Young 1963

Cont.

Species	Family*	No. of divided broods	Author
Eared Grebe *(Podiceps nigricollis)*	Podicipedidae		Harrison 1978
Great Crested Grebe *(Podiceps cristatus)*	Podicipedidae		Simmons 1974
Horned Grebe *(Podiceps auritus)*	Podicipedidae		Ferguson & Sealy 1983
Little Grebe *(Tachybaptus ruficollis)*	Podicipedidae		Cramp & Simmons 1977
Spotted Antbird *(Hylophylax naevioides)*	Formicariidae		Willis 1972
Splendid Fairy-wren *(Malurus splendens)*	Maluridae		Russell & Rowley 1988
Yellow-billed chough *(Pyrrhocorax pyrrhocorax)*	Corvidae		Cowdy 1962
Wood Thrush *(Hylocichla mustelina)*	Muscicapidae		Harrison 1978
American Redstart *(Setophaga ruticilla)*	Fringillidae		Boxall 1983
Prairie Warbler *(Dendroica discolour)*	Fringillidae		Nolan 1978
Common chaffinch *(Fringilla coelebs)*	Fringillidae		Marler 1956

Cont.

Species	Family*	No. of divided broods	Author
Smith's Longspur *(Calcarius pictus)*	Fringillidae		Jehl 1968
Five-striped Sparrow (*Aimophila quinquestriata)*	Fringillidae		Mills *et al.* 1980
Large Ground Finch *(Geospiza magnirostris)*	Fringillidae		Grant & Grant 1980
Large Cactus Finch *(Geospiza conirostris)*	Fringillidae		Grant & Grant 1980
Sharp-beaked Ground Finch *(Geospiza difficilis)*	Fringillidae		Grant & Grant 1980
Medium Ground Finch *(Geospiza fortis)*	Fringillidae		Price & Gibbs 1987
Hooded warbler (*Wilsonia pusilla*)	Fringillidae		Evens Ogden & Stutchbury 1997
Ovenbird *(Seiurus auropillus)*	Fringillidae		Hann 1937

* Family names arranged as set out in Sibley & Ahlquist (1990).

Table 1.2. A summary of the hypotheses used to explain brood division.

Hypotheses	Proposed by	Prediction	Evidence in favour	Evidence against
Reduces predation	Smith 1978; McLaughlin & Montgomerie 1985	Brood division and separation should be most pronounced when young are most vulnerable	Division formed soon after young left the nest (Smith 1978; McLaughlin & Montgomerie 1985)	Division did not decrease predation in dunnocks (Byle 1990) Division did not form till young became mobile (Moreno 1984; Harper 1985; Byle 1985)
Increases feeding efficiency	Smith 1978; Moreno 1984	Division should form when young are hardest to find Division should reduce the distance between adults and offspring Family units should maintain separate feeding areas	Division in Lapland longspurs resulted in reduced travel time (McLaughlin & Montgomerie 1985)	Fledglings were not fed at a greater rate in divided broods (Edwards 1985). Division formed when young followed adults about the territory (Harper 1985)
Reduces sibling competition	Smith 1978; Harper 1985	Food will be allocated more evenly in divided broods		No difference in weight variance in broods of robins (Harper 1985)
Advantage for one sex of adult to care for a particular sex of offspring	McLaughlin & Montgomerie 1985	Broods divided by sex	Blackbirds (Snow 1958), robins (Harper 1985) & dunnocks (Byle 1990) show evidence of dividing by sex	Bluethroats (Anthonisen *et al.* 1997) and hooded warblers (Evens Ogden & Stutchbury 1997) do not show evidence of division by sex

Hypotheses	Proposed by	Prediction	Evidence in favour	Evidence against
Results from sexual conflict between adults	Slagsvold *et al.* 1994	One sex chooses to care for the fledgling requiring the least post-fledgling care	Male blue tits increased their chances of survival by caring for the largest fledgling (Slagsvold *et al.* 1994)	
Reduces adult cheating	Magrath pers. comm.; this study	Ensures even levels of care by forcing adults to feed fledglings enough for them to survive		
Results from adult dispersion	This study	Brood division occurs as a result of the breakdown of the pair bond	Brood division associated with dispersion in Lapland longspurs (McLaughlin & Montgomerie 1985), bluethroats (Anthonisen et al. 1997) and Hooded warblers (Evens Ogden & Stutchbury 1997)	Divided broods of robins mingled freely (Harper 1985)
Results from fledgling choice	Slagsvold 1997	Largest chicks choose to be fed by the best feeder	Largest fledglings were associated with the best feeder in broods of American robins (Weatherhead & McRae 1990)	

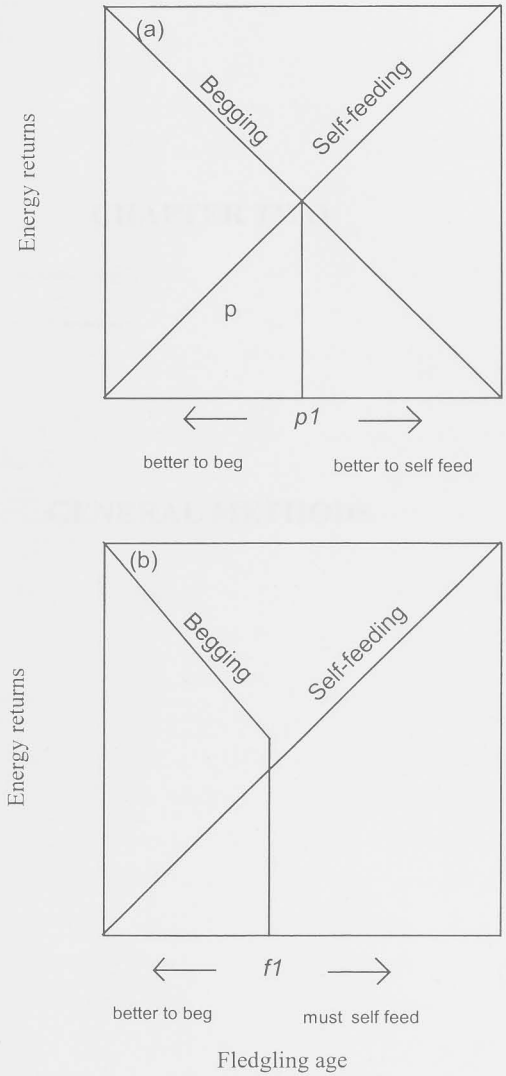

Fig. 1.1a & 1.1b. This figure shows the point at which young should switch from begging to self-foraging when (a) adults and young negotiate the length of dependence and, (b) adults are solely in control of the length of dependence.

CHAPTER TWO

GENERAL METHODS

Study Species and Site

The white-browed scrubwren, *Sericornis frontalis*, is a small (11-15g) endemic passerine in the family Pardalotidae, subfamily Acanthizinae (Sibley *et al.* 1988). It feeds primarily on arthropods found on or near the ground. It is common in eastern and southern Australia (Christidis & Schodde 1991) and breeds in a diverse range of habitats, from coastal rainforest to alpine heath (Blakers *et al.* 1984; Christidis & Schodde 1991). Adults can be sexed by plumage, as males have black lores and females have brown lores, but in their first few months the sexes are indistinguishable by plumage.

I studied a colour-banded population of *S. f. frontalis* in and adjacent to the Australian National Botanic Gardens (35° 16' S 149° 6' E), Canberra, Australia, over three breeding seasons; 1993, 1996 and 1997, with the year representing the year in which the breeding season began. My study ran concurrently with a longer term study which ran from 1992 to 1998 (Magrath & Whittingham 1997; Magrath & Yezerinac 1997; Whittingham *et al.* 1997; Whittingham & Dunn 1998; Magrath *et al.* 2000; Magrath in press). The Gardens occupy an area of 40 ha, of which 27 ha is planted exclusively with Australian native plants. Most of the remaining 13 ha is natural woodland, which is contiguous with a large area of natural habitat in which scrubwrens breed.

Scrubwrens most commonly bred in pairs (46% of groups) or in trios consisting of a socially-dominant pair and a subordinate male (44%), although 10% of groups had more than one subordinate male (Magrath & Whittingham 1997). I use the term "alpha" male to refer to either the male in a pair or the dominant male in a larger group. Only the female builds the nest and incubates, but both members of the dominant pair, and often subordinate males, provision nestlings (Magrath & Whittingham 1997). The birds are resident throughout the year, and during the breeding season territories were visited at least three times a week to document reproductive attempts (Magrath & Yezerinac 1997; Magrath *et al.* 2000). There were between 35 and 48 breeding groups in any one breeding season.

Clutches were usually initiated between August (winter) and December (summer) and most contained three eggs (Magrath *et al.* 2000). The mean

incubation period was 18.8 days and young left the nest about 15 days after hatching (Magrath *et al.* 2000).

As part of the larger study, all nestlings had a blood sample taken in the nest to enable molecular sexing, using the PCR technique described by Griffiths *et al.* (1998), although a few young from the 1993 season were not sexed. Nestlings were also uniquely colour-banded, weighed and measured when 9 or 10 days old, the oldest age they can always be safely handled.

General Observations

Observations of adults feeding fledglings were spread over the post-fledging period, and designed so that each was independent. In any one observation period, each fledgling was watched for up to 15 minutes or until it was first seen to be fed by an adult, and so was recorded as either being fed or not being fed. Observations were usually separated by at least one day, although some were collected on the same day but separated by at least two hours. Observations on most families continued until just after the end of parental care.

The focus of observations varied depending on the age of the young, which in this thesis is recorded as the number of days after young had left the nest. During the dependency period, observations focussed on adults feeding fledglings. Full details of the activity recorded during this period are contained in Chapter Three. After the end of dependency, territories were surveyed, where possible, on a monthly basis, to determine the approximate date that young left their natal territory. Sample sizes varied for each data set due to deaths of offspring and because, for some groups, insufficient data were collected.

Nestling weight

Nestlings were weighed to the nearest 0.1 g when 9 or 10 days olds and were also weighed when about six days old, although weights were collected on nestlings of every age between four and 12 days. This allowed for the fitting of a logistic growth curve to control for age differences among broods at the time of banding

(see Magrath & Yezerinac 1997). A sex-specific mass index for each nestling was calculated by fitting adjusted weight to sex and using the residuals.

Fledgling weight

I caught and weighed 60 young from 28 broods late in the period of post-fledging care in order to compare variation among young from small and larger feeding groups and to ascertain whether weight affected either the length of nutritional dependency or the timing of natal dispersal. I caught the fledglings 30 to 35 days after leaving the nest, and weighed them to the nearest 0.1 g. All young from a brood were caught between 0600-0900 h on the same day. A sex-specific mass index for each fledgling was calculated by fitting sex to weight and using the residuals.

Female age

Female age was estimated to determine whether yearlings behaved differently from older birds in regards to care of young. Female age was dichotomously classified as either a first year or not first year. Age of many females was known exactly because they were born during the longer term study. Females emigrating into the study population were assumed to be one year old at time of capture, as only 9% of older females moved territories between years once they had bred and in 15/16 of these cases females only moved one territory (Magrath in press). Only three individuals were not confidently classified as a first year bird or older.

Aggression

All interactions between adults and offspring were recorded as aggressive or not aggressive. An aggressive interaction was recorded when an adult either displaced, chased or pecked an offspring. Where possible, the colour bands of the individuals involved were recorded. As observations focussed on parental

feeding it is likely that aggressive encounters are underestimated because observations were terminated when the young was fed.

Length of fledgling dependency

The length of dependency was taken to be the midpoint of the last observation period in which the fledgling was seen being fed within 15 minutes and the first watch of a sequence of at least three watches of 15 minutes where the offspring was not seen being fed. In order to ensure a similar level of accuracy between fledglings and years, individuals were only included in the data set when the three non-feeding observations occurred within a two week period from the last time they were seen fed. Each observation was separated by at least one day in order to ensure independence.

Territory quality

A territory quality index was developed by Magrath (in press) based on the assumption that scrubwrens are more common in wet areas with dense cover (Blakers *et al.* 1984; Ambrose & Davies 1989, Christidis & Schodde 1991). Using this index, Magrath found that yearling females had a higher reproductive success on better quality territories, thus justifying the criteria used. The classification system was based on three factors with individual attributes being rated between 0-1, with 0 representing poor quality areas while 1 represented high quality areas. The first factor used was whether the breeding attempt occurred in a gully or not, with gullies being rated higher because they are generally wetter and have denser cover. Second, the breeding attempt was rated as either occurring primarily in the rainforest, in cultivated garden beds or in uncultivated areas. The rainforest is densely vegetated and well watered, the cultivated beds are regularly irrigated and the uncultivated beds are rarely or never watered. Third, territories were classified as being in the south-east, north-east, south-west or north-west. This classification approximates the slope of the land with wetter areas being found in the south-east and drier areas in the north-west. The scores were then summed to establish over-all quality and, as about one

third had scores of 1.5, one third had higher scores and one third had lower scores, they were divided into three categories representing high, medium and low quality territories.

Rainfall data

Average rainfall was calculated using data collected over 56 years by the Canberra Meteorological Office at the Canberra Airport (35°18` S, 149°12` E), about 8km from the study site.

Duration of natal philopatry

In order to determine the date of natal dispersal, I monitored all territories at least once per fortnight during the breeding season (June-January) and once per month during the non-breeding season (February-May) in 1996 and 1997. The date of dispersal was taken as the mid-point between the last time the young was seen on the territory, and the first census period when the young was recorded as being absent from the natal territory and was not seen again on that territory. Young that remained until September in the following year were considered to have not dispersed and, based previous research, young that disappeared before six weeks old were considered to have died (Magrath *et al.* 2000). The only period when the regular monthly census was not carried out was during March, April and May of 1997. It is unlikely that this would have affected my results as only five (out of 18) individuals disappeared during this time (3 females and 2 males). Unfortunately, due to time constraints, the surrounding habitat was not regularly surveyed for dispersers.

Statistical analysis

I have generally used a modelling approach in statistical analysis. Data on factors which affected observed patterns of behaviour (such as the length of fledgling dependency and natal philopatry, and the proportion of care provided by each adult in a breeding group) were unbalanced and generally replicated on one or

more levels. For example, when examining what factors affected the length of fledgling dependency, replication at the brood level had to be taken into account. To overcome this intra-brood replication I used mixed models with random and fixed effects. Continuous dependent variables were analysed using the restricted maximum-likelihood (REML) procedure while binary dependent variables were analysed using the generalised linear mixed-model (GLMM) procedure (Genstat Committee 1993). Fixed effects are used to describe the factors of interest, such as whether or not a fledgling's sex affects its length of dependency. Random effects are used to describe the effects of factors which represent a random selection of the values in some larger homogeneous population. In the above example, the brood is treated as a random effect because it represents a random selection of broods in the wider population and is not, in itself, of particular interest when examining factors which affect the variation in dependency times of young within those broods. In some instances it is also useful to obtain information on the level of variance accounted for by the random structure. This can be obtained in the above models by using the estimated variance components. The resulting output gives a correlation score which ranges between 0 (no variance accounted for by the random structure) to 1 (all of the variance in the model is accounted for by the random structure).

Models were fitted by initially including all explanatory variables of interest as fixed effects. Interaction effects were only fitted were there was an *a priori* reason for doing so. The final model was selected by sequentially dropping non-significant interactions and then non-significant factors, until only significant terms remained. To avoid confounding order effects, any term that was close to significance ($P<0.20$) was re-evaluated by adding and dropping it from the final model. All significance scores and estimated mean values are reported including any significant ($p<0.05$) terms in the fixed model. Significance for factors in the REML models were assessed by looking at the change-in-deviance between the full model, which included all significant terms, and the sub-model, which excluded the factor of interest. The change-in-deviance score was used as it represents an approximation of a chi-square distribution. Significance for GLMM models was assessed using Walds statistic calculated when the term of interest was fitted last in the model. All final parsimonious models were checked with appropriate diagnostic plots.

There were four instances in which I was interested in whether the frequency of a particular behavioural trait changed over time. These behavioural traits were recorded dichotomously as either happening or not happening. Analysis of these data was complicated because it involved replication over time of observations on the same fledgling and replication within each brood. In order to assess whether the behaviour changed over time I first grouped the data into three day periods. This converted the data series into binomial data. Then, by using a generalised linear model with a spline smoother, I was able to use the mean deviance of the fitted model to assess if there was unaccounted for structure within the final model (Genstat Committee 1993). I used the general rule of thumb that if the mean deviance was greater than two then model did not adequately account for the structure within the data and further modelling was needed. In fitting the spline smoother, I initially started with a quadratic spline and reduced the intensity of the curve if the change in deviance was not significant. In order to test if the spline smoother represented a significant non-linear fit I used the level of deviance in the final fitted model, which is approximately equal to the chi-square distribution.

In the presentation of the results, non-significant outcomes are mentioned only if they are of note. Most figures present data ($\bar{X}\pm SE$) with model predictions super-imposed. Standard errors in figures were generated from raw data, and because they do not explicitly take account of the random structure, they should not be used for statistical inference.

The GLMMs, REMLs and spline smoothers were fitted using the GENSTAT statistical package (Genstat Committee 1993). I used parametric methods where assumptions of tests were met by raw or transformed data, otherwise I used non-parametric tests (Sokal & Rohlf 1995). All tests were two-tailed.

CHAPTER THREE

PATTERN OF FLEDGLING CARE AND BROOD DIVISION

In nearly all species of birds adults provide food to young after they have left the nest. Of the few detailed studies into this period of care, some have revealed that adults preferentially feed a subset of the brood over some or all of the post-fledging period (Horsfall 1984; Moreno 1984; McLaughlin & Montgomerie 1985; Edwards 1985; Harper 1985; Price & Gibbs 1987; Weatherhead & McRae 1990). The function of such brood division is unknown, and in this chapter I aim to assess the eight hypothesis suggested in Chapter One.

The predation hypothesis suggests that brood division reduces the risk of losing offspring to predators. Three mechanisms have been suggested as to how predation might be reduced by splitting the brood. First, Smith (1978) suggested that it may be possible for adults to remain closer to offspring in a small group and so be better able to warn them of the approach of danger. Second, if fledglings in divided broods are kept further apart than those in non-divided broods it may reduce the probability of a predator finding and taking the entire brood (McLaughlin & Montgomerie 1985) and, third, I suggest that it may be harder to find individuals in smaller groups because they are potentially quieter due to reduced competition. All of the above hypotheses predict that offspring will be found apart when most vulnerable to predation and that brood division will be most pronounced during this time. There is currently no evidence that brood division reduces predation, although few studies have directly tested this hypothesis (see Chapter One).

The feeding efficiency hypothesis suggests that brood division increases the rate that young can be fed or reduces parental energy expenditure (Smith 1978; Moreno 1994). This hypothesis makes three predictions. First, if adults cared for a reduced subset of the brood they can potentially remain closer to those offspring and hence reduce both search and travel time (Smith 1978; Moreno 1984). The distance between adults and offspring could be reduced either by adults maintaining separate foraging areas or by subfamilies travelling together about the territory. Second, brood division should be strongest when young are hardest to find as this is when search and travel times should be greatest, and third, adults might maintain separate foraging areas in order to control depletion and renewal of food resources and have better knowledge of patch profitability (Moreno 1984).

This hypothesis has been directly tested only in dunnocks, *Prunella modularis* (Byle 1990), and robins, *Erithacus rubecula* (Harper 1985), and in neither study did brood division increase feeding rates. Brood division did, however, reduce travel times in Lapland longspurs, *Calcarius lapponicus* (McLaughlin & Montgomerie 1985 & 1989), and thus theoretically could have reduced adult energy expenditure or increased feeding rates, although this was not shown directly.

The sibling competition hypothesis suggests that brood division enables the equitable distribution of food to young by reducing the effects of sibling competition. This may be achieved in two ways. First, adults with fewer young to care for may be better able to remember how much they have fed each individual and hence allocate food more evenly between members of their sub-family or, alternatively, sibling competition may be reduced in smaller groups and eliminated in groups of one (Smith 1978). This hypothesis predicts that food will be allocated more inequitably as the number of young in the sub-group increases, leading to greater differences in condition between the biggest and smallest offspring. A variation on the above hypothesis is that adults of a divided brood will have perfect knowledge over the amount of food that an individual has been fed and hence be less susceptible to manipulation by exaggerated begging calls of offspring (Harper 1985).

Harper's (1985) is the only study to directly test this hypothesis and he found no difference in the variance of feeding rates of divided compared with non-divided broods. No study has tested the idea that brood division is a response to exaggerated signals but evidence from the nestling period exists to show that adults do respond positively to increased levels of begging (Bengtsson & Ryden 1983).

The division by sex hypothesis suggests three reasons why adults might care for a particular sex of offspring. One, a particular sex of young may benefit more by being fed by the adult that can provide the most food (Horsfall 1984; McLaughlin & Montgomerie 1985). Two, if adults displayed an intra-sexual foraging difference then it would be beneficial for young to be cared for by the same sexed adult (McLaughlin & Montgomerie 1985), and three, increased exposure to adults of the opposite sex might facilitate mate choice in later life (McLaughlin & Montgomerie 1985). This hypothesis requires that a relationship

will be found between the sex of the adult and the sex of the offspring. Three studies have found a relationship between the sex of the adult and the sex of the offspring (see Chapter One).

The sexual conflict hypothesis suggests that males or females might attempt to minimise the amount of post-fledgling care by choosing young that require the least effort. This hypothesis is difficult to test as it is not apparent which 'type' of offspring requires the least amount of care. Slagsvold *et al.* (1994) found that male blue tits, *Parus caeruleus*, fed the largest offspring post-fledgling and that this increased their own survival to the next breeding season. To fully test this hypothesis it would need to be shown that one 'type' of offspring does actually require less care. Further evidence for this hypothesis would be that the sex trying to minimise care post-fledging also tries to minimise care during the nestling period.

The adult manipulation hypothesis suggest that brood division might be a strategy to enforce 'even' levels of care by all adults within the group (Magrath pers. comm.). If an adult feeds one or more fledglings, but refuses to feed others, it places the other adults in the position of forcing them to provide adequate care to the remaining fledglings, or letting them die. This hypothesis predicts that broods will be divided evenly between the feeding adults. No study has tested this hypothesis.

I suggest a novel hypothesis, the adult dispersion hypothesis, which suggests that brood division is not functionally adaptive and is a result of adults feeding in separate non-contiguous areas. If adults fed a significant distance away from each other then offspring would have no opportunity to switch between feeding groups. Brood division, therefore, would become established by parental separation without it necessarily being the cause of parental separation. If this hypothesis is correct then division should occur when adults are found apart but not occur when adults are found together.

Finally, the fledgling choice hypothesis suggests that brood division might be the outcome of choices made by young, not adults. Slagsvold (1997) first suggested this idea based on findings that the largest chick was often associated with the best feeder (see review by Slagsvold 1997). However, he qualified this idea by suggesting it did not provide an ultimate explanation of brood division but rather a mechanism for deciding who would be fed by whom. I go further

and suggest that the fledgling choice hypothesis does provide an ultimate explanation of brood division and that adults might not have a preference over which young they feed. This hypothesis predicts that the most dominant fledgling will be associated with the best feeder. It also predicts that brood division should form when fledglings take an active role in obtaining food from adults and that adults will not actively exclude young from their feeding groups.

Two things stand out when discussing brood division. First, that the careless use of the term, and inappropriate sampling protocols have hampered progress in understanding why division occurs. The term brood division should be reserved for situations where adults and young are shown to form stable feeding groups throughout a significant proportion of the fledglings dependency period. In contrast to such long-term associations, it is inevitable that adults will show short-term biases in feeding young that are closer or of a known location. This, however, is not brood division. To adequately demonstrate brood division, observations need to be both independent of each other and spread over the entire dependency period.

Second, that progress towards developing a theoretical framework for understanding brood division has been limited by equating a short-term feeding bias with long-term brood division. Several hypothesis that have been suggested to explain brood division only suggest a benefit of keeping young separate or, perhaps, why there might be short term biases in feeding particular young. These hypothesis, however, do not address the issue of why a particular adult should feed a particular young throughout the duration of its dependency period. This problem will be developed further in the discussion.

In this chapter I will first document brood division by sampling behaviour over the whole period of care, and then test the above functional explanations. Previous studies have found that when division occurs it is often complete, thus precluding the possibility of directly comparing divided and non-divided broods. Furthermore, comparing divided and non-divided broods may provide misleading results as poor quality adults might be forced to divide while adults in better condition may not (Harper 1985). To overcome these difficulties I will test the assumptions of each of the hypotheses.

METHODS

Adult-fledgling interactions

Observations of adults feeding fledglings were spread over the entire post-fledging period and designed so that each was independent. In any one observation period, each fledgling was watched for up to 15 minutes or until it was first seen fed by an adult, and so was recorded as either being fed or not being fed. Observations were usually separated by at least one day (N=1490), although some were collected on the same day but separated by at least two hours (N=42). Observations on most families continued until just after the end of parental care.

For each observation of a fledgling I recorded the following data.

1) The location of the interaction. The location was plotted onto a scale map of the study site and encoded as a grid reference with a 3m precision.

2) Whether the fledgling took an active or passive role during a feed. Fledglings were scored as playing an "active role" in obtaining food if they approached the adult or were following it immediately before being presented with food. Fledglings were scored as playing a "passive role" if they were stationary and the adult brought food to them.

3) The distance between the adult and fledgling immediately before one bird moved towards the other. Distance was categorised as: 1=0.0–0.1m; 2=0.1–1m; 3=1–2m; 4=2–5m; 5=5+m. When it was necessary to use mean distances for fledglings, I converted the categories into distances by using the mid-point, with 5+m being converted to 7.5m.

4) Whether or not fledglings were stationary and together. Fledglings were considered to be together if all were within one meter of each other and considered stationary if the adults bought food to them while their positions did not change. If the fledglings were hidden in dense cover their distance apart was estimated from the location of begging calls.

5) Whether or not the adult fed the nearest fledgling and whether it avoided one fledgling to feed another. Avoidance was said to occur when an adult with food moved from a fledgling who was begging or chasing it to feed another.

6) Whether or not any aggressive behaviour occurred during the watch. Aggression could occur between siblings or between an adult and young. Aggression could take the form of one individual displacing another from a feeding site, chasing or physical contact.

Overall, I gathered sufficient data (at least 6 independent feeds per fledgling) on 33 broods to test for the occurrence of brood division (see Table 3.1 for a breakdown by field seasons). I also collected data from another 20 broods which were used in the general analyses on fledgling development (12 contained only a single fledgling (see Table 3.1 for a breakdown by field seasons), in seven I was unable to gather a sufficient sample, and in one the young died at day 24).

Care of nestlings

Parental feeding rates to nestlings were measured to test the hypothesis that fledglings may compete for the best adult to feed them. Nests were watched as part of the larger study on this population. Each nest was watched, if possible, for three (occasionally more) one-hour periods, usually at two day intervals when nestlings were between seven and eleven days old. Days on which nestlings were handled were avoided. The identity of each adult was recorded if the colour-band combination was seen, and feeds by unknown adults were allocated in proportion to identified feeds. Totals for each adult were then summed across watches and the best feeder was the one who delivered the most feeds to the nest. Observation

periods where more than half the feeds were unknown were excluded from this analysis.

Post-fledging survival and duration of parental care

As part of the larger study on scrubwrens (Chapter Two) data were gathered on the survival of all fledglings for the period 1992-1998. Territories were searched soon after fledging, and at two, four and six weeks after young had left the nest. Chicks that were alive when banded were considered to have fledged unless there was evidence that predation occurred while the young were still in the nest. I used six weeks as the final census date as adults often stopped feeding young around this time, and young can disperse soon after (Leedman & Magrath, unpublished). See Chapter Two for full details on how the duration of care was measured.

Adult removal experiment

During the 1997 breeding season I removed single adults for short periods from seven divided broods in order to establish whether adults or young maintained brood division. The aim was to remove the adult from one sub-family and observe whether the "orphaned" fledgling(s) followed and were fed by the remaining adult(s). Observation focussed on the orphaned fledgling or, when there were two orphaned fledglings who remained apart, observation time was divided equally between them. I also recorded any aggression between adults and fledglings and among fledglings (see adult-fledgling interactions section). The experiment was carried out 20 to 26 days after fledging, over three consecutive days.

This experiment consisted of: (i) pre-manipulation control observations; (ii) experimental removal; and (iii) control manipulation. The order of the control manipulation and the experimental removal were alternated between broods. During the pre-manipulation control day I observed the family for two hours. On the removal day I caught and removed one feeding adult (the first captured) for a period of one hour, during which time I watched the remaining family members. If no adult was caught within two hours I abandoned the attempt and tried again the next day. After the release of the adult, the family was watched for a further

hour. During the control manipulation I attempted to catch and release all adults. The purpose was to control for any effects of the disturbance caused by capture. If no adult was caught within two hours I made the assumption that I had created a sufficient disturbance to constitute a control. The family was then watched for two hours.

Testing for brood division

I tested sequentially for two features of brood division. First, I used a goodness of fit test on each fledgling to see whether it was fed unequally by those adults that fed it. Unequal feeding always indicated a single "primary carer" who was responsible for most of the feeds. Second, when two or three young from the same brood did have a "primary carer" I tested for statistical association in contingency tables to see if different young were fed by different adults. Analysis of a truly "divided brood" should reveal that fledglings are fed preferentially by specific adults and that different fledglings are fed by different adults. In cases where brood division did occur, all feeds by the fledgling's "primary carer" are referred to as "primary feeds", and feeds by other adults are referred to as "non-primary feeds".

RESULTS

Pattern of brood division

Brood division was the normal pattern of care for broods of two or three fledglings; 70% were divided (23/33 broods; Table 3.1). For example, in brood 151, in which three fledglings were raised by a pair, the male provided 18/19 feeds to fledgling A and the female provided 20/20 feeds to fledgling B and 15/16 feeds to fledgling C. Each fledgling was fed preferentially by one adult, and the fledglings were fed by different adults, so meeting both statistical criteria for complete "brood division". The 19 feeds to fledgling A were observed on 19 different days, with 18 days from 11 Oct to 18 Nov 93; unusually, there was also

one isolated feed on 10 Jan 94, two months after the termination of regular feeding. All feeds to the other two fledglings were observed from 11 Oct to 18 Nov 93; there were no "late" feeds. In this brood I was unable to collect records for the first week after fledging (on 2 Oct 93), but otherwise observations covered the complete period of care.

In two broods of three, brood division was incomplete, with two fledglings divided, but one fed by two adults (Table 3.1). In brood 493, fledgling A was fed exclusively by the male and fledgling C exclusively by the female, but fledgling B was fed by both adults (7 feeds by the female, 3 by the male; chi-square = 1.6, df = 1, p =0.2). In brood 551, a group with two males, fledgling B was fed exclusively by the beta male, fledgling C almost exclusively by the alpha male (16/17 feeds), but fledgling A was fed by both males (4 feeds by the alpha, 10 by the beta; chi-square = 2.6, df = 1, p = 0.1).

Most fledglings had "primary carers", even in broods that were not divided (Tables 3.1, 3.2). Amongst broods of one, the primary carer was the female in five broods, the alpha male in four broods and the beta male in one brood; only two single fledglings did not have a primary carer (Table 3.2). In larger broods with no brood division the alpha male was usually a primary carer (Table 3.2), although some members of the brood could be shared with other adults (Tables 3.1 & 3.2). For example, in brood 189, fledgling A was fed exclusively by the alpha male, fledgling C nearly so (16/18 feeds), but fledgling B was fed by the female (1 feed), alpha (7 feeds) and beta (5 feeds). With two possible exceptions of the 45 broods observed in detail, two broods of one (brood 143 and 417), there was no family in which all fledglings were fed equally by all adults.

Brood division was most likely to occur during final nesting attempts for the season (Fisher exact: p=0.03). In early nests, 4/10 broods of more than one young divided while, in final nesting attempts 19/23 were divided.

Does brood division decrease predation?

If brood division occurred to reduce predation then it should be strictest when the probability of predation is the highest. Disappearances in scrubwrens peak in the first two weeks after young leave the nest and then decline rapidly (Contingency table: X^2_2=260, P<0.001; Table 3.3). In this analysis, each period is treated as an

independent data set and, therefore, the probability that a fledgling survives each period is considered as independent of its probability of surviving the last period. Although this assumption is probably not strictly true, it is unlikely, considering the magnitude of the difference between periods, to affect the conclusion that predation is higher in the first two weeks of life than during any other period. All young alive in the nest after banding are included as having fledged unless there was evidence of nest failure. This analysis included all young that hatched between 1992-1998.

It is possible that brood division did not occur to reduce the absolute level of predation, but rather to reduce the chances of losing all young in a single predation incident. This hypothesis predicts that young will be kept separate when most vulnerable. Young, however, remained stationary and together, that is within at least one metre of each other and in thick vegetation, during the first few weeks after leaving the nest (Fitted spline smoother: $X^2_{1,7}=170.8$; $p<0.001$; Fig.3.1). Although this analysis uses pooled observations, there was no evidence that there was unaccounted for structure within the data (residual mean deviance when a factor one spline smoother fitted=1.4).

Despite the high risk of predation in the first two weeks, broods were less divided during this period: adults of broods that became divided often fed fledglings other than their eventual "primary fledglings" during this time and during the final stage of fledgling dependency (Fitted spline smoother: $X^2_{3,14}=84.2$; $p<0.001$; residual mean deviance when a factor three spline smoother fitted = 0.92; Fig.3.2).

The finding that brood division is weakest when predation rates are highest suggests that brood division does not primarily occur to reduce predation rates, otherwise brood division might be expected to occur earlier. It is possible, however, that the rapid decline in fledgling disappearances after week two is caused by brood division. If this hypothesis is correct, then predation rates of single fledglings should not decline after week two because a brood of one does not change from being undivided to divided at that time. I tested this idea by looking at temporal changes in the probability of death of fledglings from broods of one or more. Single fledglings had the same dramatic decline in mortality after week two as did fledglings from larger broods, thereby showing that the

temporal change in mortality in larger broods was not caused by brood division (Table 3.4).

Most deaths in scrubwrens were probably due to depredation rather than starvation, and the most common predator was probably the pied currawong, *Strepera graculina*, a large omnivorous bird. Currawongs have been seen hunting fledglings on several occasions, and the colour bands of both nestlings and fledglings have been found in their regurgitated pellets (Prawiradilaga 1996; Magrath pers. comm.). By contrast, nestlings rarely died of starvation, which suggests fledgling disappearances are also not due to starvation (Magrath & Yezerinac 1997).

Does brood division increase parental feeding efficiency?

There are several mechanisms that might allow brood division to increase the rate at which young are fed. Adults with fewer young to care for may be better able to remember their locations and hence reduce time spent searching for young when they have found a food item, or they may be able to remain closer to those young and hence reduce travel time. Evidence from my study, however, suggests that both search and travel time are minimal and not reduced in smaller family units. Young, both in broods where the primary career fed a single fledgling and where the primary career fed two fledglings, were mostly less than one metre away from the adult immediately before the feeding interaction (Fig.3.3), suggesting that adults did not search for young in order to feed them. Furthermore, when the distance apart scores were converted to a continuous measure and averaged for each fledgling, they did not differ between the different sized feeding groups (Wilcoxon test: X^2=1.7, N_1 (one fledgling)=51, N_2(two fledglings)=26, df=1, p=0.19). The median distance (inter-quartile range) between the adult and fledgling in groups where the adult fed a single fledgling was 0.8m (0.45 – 1.39m), while in groups where the adult fed two young it was 1.09m (0.53 – 1.52m). Data in the above analysis and figure were restricted to observations collected after young were more than two weeks old, as before then brood division was not fully established in many groups (Fig. 3.2).

Further evidence that search and travel time was minimal and not reduced by brood division comes from the finding that as young got older they

increasingly played an active role in obtaining food from adults (Fitted spline smoother: $X^2_{2,14}$= 177.1, P<0.001; residual mean deviance when a factor two spline smoother fitted=1.6; Fig. 3.4). If brood division primarily occurred in order to reduce search and travel time, then it should be less pronounced when young actively pursued adults and more pronounced when young played a passive role. As already mentioned, however, after fledging young were mostly found stationary and together, but brood division did not occur during this period (Fig. 3.1).

An alternate way in which brood division might increase parental feeding efficiency is if it allowed adults to specialise in a particular part of the territory and hence be better able to control the depletion and renewal of food resources and have a greater knowledge of patch profitability. However, there was no evidence that adult scrubwrens restricted their activity to particular parts of the territory in any of the 23 broods that were divided. Figure 3.5 shows a sub-sample of feeding locations of fledglings in six randomly chosen families that divided. Figure 3.5 suggests that there might be some peripheral areas of the territory that are used more frequently by some subfamilies than others, but in all cases the distributions of feeding locations are mostly overlapping.

Finally, different feeding groups from the same brood remained near each other. If brood division occurred to increase feeding efficiency by reducing parental feeding costs then, when feeding groups came together, young should, theoretically, be able to switch between feeding groups. Adults should not object to this swapping as long as it allowed them to continue feeding young in separate groups. This however, does not happen: fledglings from one subfamily were within 5 metres of fledglings from another subfamilies about 60% of the time (Fig. 3.6) and no switching between groups was seen (Table 3.1). Figure 3.6 may even exaggerate the distance between groups as it was difficult to identify individuals close together in vegetation making it likely that these situations are under-represented. Unfortunately I am unable to estimate the magnitude of this bias as I collected data on distance apart when first fed, not when first seen. I restricted this analysis to family units that contained a single young, as it was not always possible to see the colour-bands of the nearest sibling, and hence for sub-families of two fledglings, distinguish if the nearest sibling was from the same family unit or another.

Does brood division occur to reduce the effects of sibling competition?

According to the sibling competition hypothesis, the difference in fledgling mass should be greatest among fledglings fed by the same primary carer, compared with fledglings fed by different primary carers. In order to test this prediction I used two methods. First, I calculated the intra-nest correlation of fledgling weight of young from broods fed by different primary carers and those fed by the same primary carer by using the variance components from a REML model, controlling for sex. Second, using mass residuals controlled for sex, I looked at the correlation between the largest and smallest fledgling in broods where each fledgling was fed by a different adult and broods where two fledglings were fed by the same adult. Both methods found that the mass of young fed by the same adult was more similar than the mass of young fed by different adults, which goes against the sibling competition hypothesis. The intra-nest correlation of fledgling weight, using variance components from the REML model, was greater for young in broods where two offspring were fed by the same primary carer ($R=0.44$, N=10 broods) than for young in broods were all young were fed by a different primary carer ($R=0.0$, N = 8 broods). These results were supported when mass residuals of the largest and smallest young were compared. Broods where young were fed by different adults showed little relationship in weight (ANOVA: $F_{1,7}=3.2$, $p=0.12$, $R^2adj=0.24$; Fig. 3.7a) as compared to broods where two young were fed by the same adult (ANOVA: $F_{1,9}=40.3$, $p<0.001$, $R^2adj=0.81$; Fig.3.7b). The difference between the two figures is more extreme when the potential outlier at the bottom of Fig. 3.7a is removed, thus further strengthening the case that there is little or no correlation between the mass of young when they are fed in divided broods but a strong correlation between their mass when fed by the same adult.

Is brood division a result of adults showing a preference for feeding a particular sex of young?

There was no association between the sex of the primary carer in divided broods

and the sex of primary fledglings. Females cared for 13 female and 6 male offspring while males cared for 22 female and 16 male offspring (Fisher exact: X^2=0.6, df=1, p=0.44). However, of the divided broods that I watched until independence, 8 out of 23 were all of the same sex, so no choice was possible. To test for unexpressed preferences, I examined divided broods in which there were both sons and daughters, and in which the female cared for at least one fledgling. I classified these broods as either 'same-sex' or 'different-sex' broods. In broods of three, I scored the unique sexed young. Again there was no preference; there were 7 "same-sex" broods and 5 "different-sexed" broods. Similarly, amongst broods containing a single fledgling where there was a primary carer, there was no hint of preference. Two daughters were cared for by mothers and two by alpha males and three sons were cared for mothers and three by males (one a beta male).

Is brood division a result of sexual conflict between adults?

Males or females may choose to feed offspring that require the least amount of care. Although I found evidence that alpha males tended to feed the largest nestling after it had left the nest (15/22 largest nestlings; chi-square test:X^2_1=2.91; df=1, p=0.09), largest nestlings did not require more or less care than other nestlings. Heaviest chicks were cared for, on average, for 44.5 days (N=26, SE±0.85) compared to 43.4 days for other chicks (N=36, SE±1.27; t-test: t_{57}=0.78, P=0.44). Thus there was no evidence that alpha males or females were choosing young requiring a shorter period of care. It is possible, however, that largest fledglings required more food in absolute terms. This idea was not tested as it was not possible to record feeding rates to individual fledglings.

Does brood division enforce "even levels" of care between adults?

Brood division frequently results in one adult feeding more young than another. One parent fed two offspring in eight of the 13 divided broods where three young were present. The alpha male fed the subset of two young in six broods, the female in one brood and the beta male in the other brood. Further evidence that brood division did not result in an even distribution of labour comes from the

finding that breeding adults are able to opt out of care completely when the brood divides. Five females and one alpha male did not feed any young when the brood was divided. Of the females that opted out of care, only two were seen attempting another nest.

Was brood division simply a result of adult dispersion?

There is no evidence to suggest that brood division is a result of adult dispersion. Not only did adults use the entire territory throughout the post-fledging period (Fig. 3.5), but family sub-groups were within five meters of each other in over 60% of the feeding observations (Fig. 3.6).

Was brood division a result of fledgling choice?

The hypothesis that brood division is a result of fledgling choice makes a number of predictions. First, that division will become established as young take an active role in obtaining food from adults. Second, that the most competitive young should "choose" to be fed by the best feeder and may, therefore, actively exclude other young from that feeder. Conversely, if brood division is a result of fledgling choice, adult behaviour will not play an active role in its establishment or maintenance. Therefore, the fledgling choice hypothesis also predicts that adults will display little aggression towards non-primary fledglings and will usually feed the closest young to them when they find food items.

The first prediction, that brood division would become established as young took an active role in obtaining food from adults, was true in scrubwrens. As young got older, the number of feeds to non-primary fledglings decreased (Fig. 3.2) and the proportion of feeds where young played an active role in obtaining food increased (Fig. 3.4).

Larger young were also fed more by the best feeder; fledglings that had been the largest nestling were more often cared for by the adult that had fed the nestlings at the greatest rate (16/21 divided broods; chi-square test: $X^2_1=5.76$, df=1, P=0.02). There was also a trend for alpha males to feed the fledgling that had been the largest nestling (15/22 largest nestlings; $X^2_1=2.91$: P=0.09), but this result may have occurred because alpha males tended to be the best feeder at nest;

in 20 nests alpha males provided the most food, in eight nests females provided the most food while in another 10 nests it was the beta male (five nests were excluded because two birds shared equal best status and two nests excluded because feeding data were missing). I used a loglinear model incorporating both feeding rate at the nest (best or not), adult status (alpha or not) and an interaction term, in order to disentangle which was the most important explanatory variable. After dropping non-significant terms, feeding rate (best or not) had the biggest effect on who fed the largest fledgling (Logistic regression: $X^2=8.47$, $p=0.004$). In the model containing feeding rate and adult status, the status of the adult was not significant ($X^2=2.1$, $p=0.15$) and nor, when included in the full model, was the interaction effect ($X^2=1.0$, $p=0.31$).

In broods of two or more, interactions among young might influence the association between best feeder and weight as a nestling. I therefore examined associations in families with broods of one. Single chicks fed by either the female or alpha male were always fed by the one who was the best feeder at the nest (Goodness of fit test: $X^2=7$; $p<0.01$; $N=7$). In four cases this was the female, in three it was the alpha male. Three cases were excluded; in one brood feeding data at the nest were missing (nest 198), in one the female died (nest 550) and in the remaining brood the fledgling was fed by the beta male (nest 420). Beta but not alpha male care depends on paternity (Whittingham & Dunn 1998) so the single beta primary carer was excluded from these analyses. If, however, the best feeder was chosen from all birds that fed young at the nest then there is no relationship between single chicks being fed by the best feeder after leaving the nest (3/8), as in five nests the beta male provided the most food. The extra brood in this analysis comes from the addition of the brood where the beta male fed the single fledgling.

Although biggest fledglings were more often fed by the best feeder, there was no evidence that they were maintaining division by excluding other fledglings from their feeding adult. I only saw five cases (from 4 broods) of aggression between fledglings within the same brood; two were between fledglings within the same sub-family, two were between fledglings from different sub-families and the colour bands of the remaining incident were not seen. My results, however, probably underestimate the extent of aggression within families since my observation protocol focussed primarily on parental

feeding and not on other interactions. Further evidence against the idea that largest fledglings actively excluded others from their feeding adult comes from the finding that of the eight divided broods where one adult exclusively fed two fledglings, the largest fledgling was in the shared family on four occasions.

There was also no evidence that adults maintained division by aggression, as predicted in the fledgling choice hypothesis. Out of 1835 observations (from 105 fledglings from 53 broods) taken when young were eight weeks or younger (only two feeds were seen after this time) only 32 (from 16 fledglings from 12 broods) showed evidence of aggression. Four of those observations (each from different broods) were recorded in the first four weeks after leaving the nest while the remaining 28 (from 14 fledglings from 10 broods) occurred in the final four weeks (Fisher exact: $p<0.001$), suggesting that aggression is associated with "weaning" and not the establishment or maintenance of brood division. There were 10 cases (from 6 fledglings from 5 broods) of aggression by an adult towards its "primary fledgling" and 13 cases (from 9 fledglings from 8 broods) by an adult towards another adult's "primary fledgling".

The removal experiment supported the results of the general observations that adults did not maintain brood division through aggression to non-primary fledglings. In 6/7 removals, orphans followed the remaining adult, but the adult was never aggressive towards the fledgling.

Further evidence that adults did not express a preference for feeding a particular offspring comes from the finding that adults nearly always feed the closest fledgling (615 out of 631 feeds, involving 56 fledglings from 22 broods of two or three fledglings). The 16 exceptions involved 14 fledglings from 8 broods. Because I did not record the identity of the fledgling that was nearest but not fed, I cannot directly say if adults avoided fledglings from other family groups in order to feed fledglings from their own. However, if the analysis is restricted to broods where all fledglings are exclusively fed by different adults then adults fed the closest chick in 149/151 observations. In five of those observation adults fed chicks that were not their primary chicks, while in the two cases where adults fed chicks who were not the closest, they did feed their own young. This result shows that adults nearly always feed the nearest fledgling and that fledglings are most often near their primary adult when they find the food item.

DISCUSSION

Occurrence and duration of brood division

Brood division was the most common pattern of care in scrubwren broods in which more than one adult fed two or more offspring. In most cases this meant that each fledgling had a single "primary carer" that provided all or most of the feeds to that fledgling for the majority of the period of post-fledging care. In many cases this resulted in each adult feeding a single fledging, but in broods of three, one adult may care for two young and the other may care for one fledgling. In rare cases, one fledgling in a brood of three was cared for by two adults, each of which exclusively cared for another fledgling. Similar patterns of partial division have been found in blackbirds (Snow 1958; Edwards 1985) and robins (Harper 1985). In one family of blackbirds, the female fed one offspring almost exclusively (8/9 times) the male fed another, while the remaining two chicks were shared almost equally between the two adults (Edwards 1985).

Like several other multi-brooded species (Harper 1985; Edwards 1985; Byle 1990; Zaias & Breitwisch 1989), brood division in scrubwrens was more common later in the season, with almost 83% (19/23) of final nesting attempts being divided while only 40% (4/10) of early attempts were. Byle (1990) found similar results in the dunnock; all late season broods (5/5) were divided but only about half (7/12) of the early broods were (Byle 1990). In blackbirds (Edwards 1985) and robins (Harper 1985) the results were more extreme. In blackbirds, 35/43 early broods did not divide while nearly all final broods did. In robins, 1/5 early broods divided while 4/5 final broods did. Brood division is, presumably, less common earlier in the season because, rather than caring for young, females put their effort into re-nesting.

The difference between species where division commonly occurs in early broods and where it rarely occurs in early broods may be related to the breeding system. In cooperative breeding species such as dunnocks, early broods can divide because extra adults can help feed offspring, while the female goes on to re-nest. However, in monogamous species such as blackbirds, the female can

reduce her intra-nest interval by giving the male exclusive care of the offspring, hence precluding division in all but the last nest of the season (Edwards 1985).

The delay between leaving the nest and the formation of brood division in the white-browed scrubwren is long compared to other species studied. Brood division became established during the first two weeks after fledging, after which it was maintained throughout the following four weeks and then broke down near the end of post-fledging care. Brood division in dunnocks formed between 0-4 days after leaving the nest (Byle 1990), in northern wheatears it was between 3-8 days (Moreno 1984) and in blackbirds it was between 0-10 days (Edwards 1985). Furthermore, in several other species brood division occurred within a day or two of leaving the nest (e.g. Nolan 1978; McLaughlin & Montgomerie 1985; Byle 1990; Anthonisen *et al.* 1997; Evans Ogden & Stutchbury 1997).

If young influence the commencement of division, division should occur later in species that mature more slowly. In scrubwrens, the average length of dependency is about 45 days, while for species such as blackbirds, dunnocks, wheatears, and Lapland longspurs, the average length of dependency is less than four weeks. This difference in the commencement of brood division could, therefore, be a result of scrubwrens long period of dependency. Another possible explanation for the difference in timing of the commencement of brood division between species may concern parental behaviour. Adults in species such as Lapland longspurs (McLaughlin & Montgomerie 1985 & 1989) use different parts of the territory after young have left the nest and, therefore, brood division would be expected to occur earlier than in species such as the scrubwren, where adults do not divide the territory between them.

Scrubwren fledglings usually had "primary carers", even in broods of one and others that were not divided, and there was never equal feeding of each fledgling by each adult (with two possible exceptions). In some species, however, members of some broods are fed equably by adults. For example, in one brood of American robins, *Turdus migratorius,* two fledglings were fed equally by both the female and the male while the remaining fledging received most of its food from the male (Weatherhead & McRae 1990). In European robins the situation is similar, with one brood showing evidence that both the male and the female fed all fledglings equally (Harper 1985). These examples are the exceptions, however,

with the predominant pattern found across most species that divide being similar to that found in scrubwrens; that is that most young have single primary carers.

I now consider each hypothesis for the function of brood division. Testing some hypotheses must be done indirectly in scrubwrens because divided broods cannot be compared with "non-divided" broods; there were no broods in which all adults fed all young equally. In any case such a comparison, were it possible, could be confounded by other variables. Instead my approach is to test predictions of hypotheses, even if indirect.

Predation hypothesis

I found no support for the hypothesis that brood division is an adaptation to minimise the risk of depredation. The predation hypothesis predicts that brood division should be strictest when the risk of predation is greatest, but I found the opposite. Fledglings were much more likely to die in their first two weeks out of the nest, probably due to depredation, yet this was the period when brood division was weakest.

It could, however, be argued that the drop in mortality after week two was the result of brood division. This also appears unlikely as broods of one, which can not divide, show the same decline in mortality as do broods of two or three fledglings. This result would not be expected if the decline in predation was a result of brood division and suggests that the sudden drop has more to do with fledgling development.

It is also unlikely that brood division occurs to reduce the chances of losing all young in a single predation incident. The period when a predator might take all young in a single predation event occurs soon after they have left the nest, a period where young remain stationary, together and are poor fliers. But, as previously stated, brood division is weakest during this time. After this period young become mobile and the chances of a predator taking all in a single event is diminished.

Finally, no mechanism for an effect of brood division on depredation seemed probable. There was no evidence that young were kept separate to minimise sibling competition (below), that larger groups of fledglings were further from adults, or that members of separate subfamilies were kept strictly

apart. Only one other study has directly tested the predation hypothesis and it found no evidence of reduced predation between divided and non-divided broods (Byle 1990). Others studies have simply suggested brood division could be related to depredation because young were generally found apart (McLaughlin & Montgomerie 1985; Evens Ogden & Stutchbury 1997).

A general problem with the "predation hypothesis" and several other hypotheses (below) is that it is not a complete explanation for brood division. One suggested mechanism is that depredation is reduced by keeping young in different locations, but it does not explain why specific adults feed specific young (Anthonisen *et al.* 1997). However, given that young are in different locations, brood division itself may then arise if adults feed specific young to reduce their travel time while foraging and the time taken to find young and deliver food (Moreno 1984; McLaughlin & Montgomerie 1985; Anthonisen *et al.* 1997). In other words, both depredation and feeding efficiency must work together.

I suggest that the theoretical problem with this hypothesis, and some others, is even greater. A combination of keeping young apart and increasing feeding rates only explains why there might be short-term biases in feeding of specific young by specific adults, but it does not explain why the same subfamily should be stable throughout the period of care. I believe it is critical, therefore, to consider "feeding biases" and "brood division" as separate, although related, phenomena.

Feeding efficiency hypothesis

The feeding efficiency hypothesis appears not to explain brood division in scrubwrens. First, sub-families did not form sub-territories, so adults did not reduce travel time, or increase knowledge of a small area of habitat in that way. Second, brood division is unlikely to assist adults to remember the locations of individual young. Young are likely to be most difficult to find in the first two weeks after fledging, when they are usually well-hidden and are least active in acquiring food from adults. By contrast, older fledglings often follow adults, and take an active role in getting food from them and so should be easy for adults to find. If this mechanism were important, brood division should be strongest early in the post-fledging period, but I found the opposite pattern. Third, the distance between adults and young immediately before a feed was no different if an adult

was caring for a single fledgling or two fledglings, and they were usually within one meter. Thus caring for a smaller group of young does not appear to reduce travel time.

There is evidence from two other species that brood division can break down when food is abundant, but this may not be because brood division improves feeding efficiency. Price and Gibbs (1987) showed that in normal years brood division occurred in both the cactus finch, *Geospiza conirostris*, and the medium ground finch, *Geospiza fortis*, but in a year of super-abundant food supply, the fledglings were more likely to be fed by either the male or by both parents. Harper (1985) found that brood division broke down in European robins when they were provided with abundant food. These results do not, however, discriminate among the feeding efficiency, fledgling competition or fledgling choice hypotheses, as all predict that brood division should be weakest when food supply is unlimited (Slagsvold 1997).

Only one of the mechanisms for increasing feeding efficiency can in principle explain brood division as distinct from short-term biases in feeding. If intimate knowledge of a sub-territory by the feeding adult increases the efficiency of exploiting resources, and the sub-territories are sufficiently far apart to stop young from switching between feeding groups, then sub-families should be stable. The other mechanisms do not require the same adults to care for the same young every day, but could explain short-term biases.

Fledgling competition hypothesis

My results refute the hypothesis that brood division reduces the effects of sibling competition by keeping young separate and thereby enabling each young to get an equal share of food. Contrary to this hypothesis, I found that young cared for by the same primary carer were more similar in weight late in the period of care than those that were cared for by different adults. This finding suggests that brood division might, in fact, increase weight inequality because adult feeding ability potentially has a greater effect on fledgling weight than does sibling competition. It would appear, therefore, that the most optimal way to distribute food evenly to young would be for all adults to feed all offspring and thus eliminate the effects of parental quality on the amount of food that young receive. An extension of this

hypothesis is that adults might divide young so they can differentially allocate food to individuals, perhaps preferring to feed some young more than others. This hypotheses also seems unlikely. There is no particular reason why adults should have to divide their brood in order to preferentially feed certain brood members. Again, it would seem easier for adults to differentially allocate food if they fed all young rather than only a subset. I cannot refute the hypothesis that primary carers have perfect knowledge of how much food each fledgling has received and so would be less susceptible to offspring manipulation. I was unable to test this hypothesis directly as I was unable to obtain feeding rates and, therefore, unable to detect if adults responded to increases in begging levels.

The only other study to test the sibling competition hypothesis also found that brood division did not reduce the variance in weight among offspring (Harper 1985). Neither of the suggested mechanisms to reduce the effects of sibling competition can explain brood division as distinct from short-term biases.

Division by sex?

Broods were not divided by sex; there was no tendency in scrubwrens for adults to care for fledglings of the same or different sex. This was true even in broods in which there were both sons and daughters. Scrubwrens are thus similar to bluethroats where 14/24 adults fed young of the same sex while 10/24 fed young of the opposite sex (Anthonisen *et al.* 1997).

I consider it unlikely that brood division could be strictly by sex in any species, because it would be costly. For example, in a brood of all sons or all daughters, one adult could be "forced" to care for all young, which seems unlikely to be adaptive. Furthermore, if an adult died, young of the "wrong" sex would be abandoned (Snow 1958). A further problem with this hypothesis is that it can not explain why single sex broods divide at all. If division is simply a result of a preference by adults, then single sex broods should either be fed by one adult or not be divided. In scrubwrens, about 40% (13/33) of broods of two or more contained only one sex and of those eight divided.

Sexual conflict hypothesis

Although the trend towards alpha males feeding larger young in scrubwrens was consistent with the "sexual conflict" hypothesis, the trend was probably a side effect of parental feeding rate. The sexual conflict hypothesis suggests that brood division arises because males choose to look after fledglings that require the least investment, leaving females to look after young requiring more care. In a review of studies of parental care, Slagsvold (1997) found that males tended to feed larger nestlings and fledglings preferentially, and in previous work suggested that larger young require less care (Slagsvold *et al.* 1994). In scrubwrens, alpha males tended to feed fledglings that had been largest in the nest, but the trend appeared to arise because alpha males tended also to be the best feeders at the nest.

If the sexual conflict hypothesis was correct then males should minimise investment at all stages and larger fledglings should require less parental effort. This is contrary to the findings of this study. Larger fledglings were not dependent on parental care for less time and scrubwren alpha males, on average, provide more food to the nest than females (Magrath & Yezerinac 1997) and also provided a higher proportion of care to fledglings (see Chapter Six). Furthermore, in four out five broods where the alpha male and female divided three chicks between them, the alpha male cared for two offspring.

Adult manipulation hypothesis

It is unlikely that brood division in scrubwrens could arise to enforce even levels of care by adults. Frequently broods of scrubwrens consist of uneven numbers of young (Table 3.2). In many of these situations, one adult feeds more fledglings than its partner. There are also several cases where one adult, mostly the female, does not care for any offspring in final broods, leaving the remaining adult or adults to make up the shortfall. If "even" care was a priority then it would be more likely that all adults would feed all young within the same vicinity so they could monitor how much others are feeding and adjust their levels accordingly (Houston & Davies 1985).

Adult dispersion hypothesis

Brood division was not a result of parental dispersion in scrubwrens. After young left the nest, adults continue to use the same territory for feeding young. There was also no evidence that adults specialised in particular parts of the territory. Further, in over 60% of feeding observations family units were within five meters of each other, allowing young to freely move between feeding adults if there were no other constraint but distance.

The Fledgling Choice Hypothesis

Do fledglings or adults maintain brood division?

Fledgling scrubwrens play an active role in maintaining brood division. Several sources of evidence support this conclusion:

(1) The fledgling choice hypothesis predicts that brood division will occur when young take an active role in obtaining food from the adults. This was the pattern in scrubwrens. As fledglings became more active in seeking food from adults (Fig. 3.4), the percentage of feeds by adults other than the eventual "primary carer" declined rapidly (Fig. 3.2).

(2) When a fledgling's primary carer was temporarily removed, the "orphaned" fledgling followed another adult.

(3) If fledglings make active choices, more dominant or active young should choose the best adult to provide for them. I found that the fledglings that had been the heaviest in the nest had the best feeder as primary carer. This supports the hypothesis that fledglings take an active role, assuming that these adults were also investing more care in fledglings and that bigger young have "first choice" of which adult to choose as their primary carer (see also below).

(4) Adults did not maintain brood division through aggression. I only saw 32/1835 instances of aggression during feeding, overall aggression was equally

directed at primary chicks and non-primary chicks and most cases of aggression occurred during the later half of dependency, suggesting that it was associated with weaning rather than the establishment or maintenance of brood division. Further, in the removal experiment, adults were never aggressive to "orphaned" fledglings that followed them.

(5) Adults nearly always fed the first fledgling they encountered, suggesting lack of choice.

Overall, the evidence that fledgling scrubwrens play an active role in maintaining brood division is compelling, but evidence from other species does suggest that adults may also have an active role. When young white-throated sparrows, *Zonotrichia albicollis*, were caged separately just before the time of fledging, adults directed feeds to particular young (Kopachena & Falls 1991). These feeding preferences remained in some adults when young were switched between cages; adults appeared to be able to recognise individual young and fed them preferentially. Further, although parental aggression is not used to maintain division in scrubwrens or in robins (Harper 1985), it does appear to be used as a proximate mechanism in some species. In coots, *Fulica atra*, there was a negative correlation between parental aggression towards a particular chick and the number of times an adult fed that chick (Horsfall 1984). Adults appeared to be controlling the proximity of offspring by using aggression and hence controlling brood division.

Basis of fledgling choice

The biggest chicks appeared to choose the best adult to feed them, but how did this happen? I saw very little aggression among siblings, which might be expected if fledglings competed for the best feeder. I consider three possible answers. First, dominance hierarchies may be sorted out very early on, perhaps even in the nest (e.g. Drummond & Osorno 1992), and subsequently do not need to be maintained by overt aggression. However, if this is the case, it is surprising that biggest young do not prevent others from choosing the same primary carer. Second, the hierarchies and hence aggression might have been too subtle for me

to observe. The dominance structure between the alpha and beta males is easily detected in the field but it is possible that between fledglings it is not. Third, brood division might be "ideal free", but with choices being made first by bigger chicks, perhaps because they are developmentally capable of following adults sooner. This hypothesis suggests that fledglings distribute themselves among adults, who are basically mobile feeding stations. The biggest chick chooses the best feeding station (i.e. adult), the next chooses another feeding station, and so on. If two adults feed three young, the third fledgling should again choose the best feeder, explaining the trend found in scrubwrens and American robins (Weatherhead & McRae 1990) that best feeders cared for more fledglings. This mechanism is consistent with our behavioural data, and should result in stable brood division.

American robins are the only other species where convincing data show that largest young are associated with the best feeder after fledging (Weatherhead & McRae 1990; Slagsvold 1997). Out of eight broods that were watched in detail, the largest fledgling was always fed by the adult that provided the highest proportion of food. In four cases the best feeder was female while in the remaining four it was male. Data on two broods of four provide further evidence for this conclusion. In one brood the male provided only 30% of feeds post-fledging and also only fed the smallest chick. In the other brood, the male provided 70% of total feeds seen and fed the two largest chicks.

What is the function of brood division?

Evidence from my study suggests that brood division is not a parental strategy designed to maximise reproductive success (Table 3.5). Table 3.5 summarises the evidence against each of the parental benefit hypotheses and suggests that the gains of most of the suggested mechanisms could be achieved by a more temporary feeding bias. One possible reason that temporary division is not used is that division might need to be all-or-nothing. If adults switched young on a regular basis then young would learn that all adults are a potential food source and hence, when mobile, would follow all adults that had food. This may eliminate any benefits of brood division. Even if this were the case, results from this study still do not support the predictions of the functional hypotheses. It is

clear, however, that brood division is an active strategy. Family groups forage in the same area and are often found in close proximity, providing ample opportunity for members to swap between feeding groups.

Slagsvold (1997) suggested that young might be choosing which adult to feed them but went on to say that this only explained how division formed not why. I suggest that the fledgling choice hypothesis can explain both the how and why of brood division. I suggest that the reason family units do not break down is that offspring chose which adult to feed them because they are attempting to maximise their food intake. Once established, no young can improve its situation by swapping. Whether this is in the adult's interests is not clear. There is no evidence that brood division increases reproductive success or any mechanism that may potentially enhance reproductive success in scrubwrens. However, there is also little evidence that adults attempt to prevent division, suggesting that it is not too costly. It could be argued that they have no choice and cannot control the effects of sibling rivalry but results from coots clearly show that adults can control the proximity of offspring through targeted aggression (Horsfall 1984). I suggest that it is not in the interest of adults to control the distribution of food to young. Indeed, doing so would be costly as adults would need to expend energy in searching for and travelling towards young, whereas operating by a rule of feeding the nearest offspring would eliminate these costs. Results from my study support this conclusion. Brood division forms and strengthens as young gain mobility, and as young gain mobility they are most often found pursing adults for food. Feeding any but the nearest young would, therefore, be inefficient.

It is possible, however, that brood division has other functions in other species. In coots, for example, there is good evidence that adults control the proximity of young and hence who they feed (Horsfall 1984). In bluethroats, adults do not forage near each other (Anthonisen *et al.* 1997). Such separation would ensure that division occurs as young would be unable to swap between family groups. But in species such as the white-browed scrubwren there appears to be no barrier, either behavioural or spatial, and there appears to be no direct benefit to the adult. Fledgling choice is the most parsimonious explanation of why brood division occurs in this species.

Table 3.1. Number of independent feeds by adults to fledglings in broods of white-browed scrubwrens. Fledglings are arranged in order of nestling weight, with young of equal weight being denoted by =. Adult rank is represented by (F) female, (Am) alpha male and (Bm) beta male. Nests are ordered by season and date within the season

Nest	Date of Fledging	Final nest	Fledgling A					Fledgling B					Fledgling C					
			Adult			Sex	Sig[1]	Adult			Sex	Sig[1]	Adult			Sex	Sig[1]	BD[2]
			F	Am	Bm			F	Am	Bm			F	Am	Bm			
129	23 Sept 93	N	3	5		M	NS	0	10		M	*						NS
143	25 Sept 93	N	0	3	7(7)[3]	F	NS											
138	15 Oct 93	N	11	5		M	NS	0	18		F	*						
151	15 Oct 93	N	1	18		M	*	20	0		M	*	15	1		F	*	*
194	13 Nov 93	Y	0	24	2	F	*	1	0	25	F	*	15	7	1	F	*	*
178	15 Nov 93	Y	4	16		M	*	20	1		F	*						*
184	17 Nov 93	Y	1	19	3	F	*	17	0	1	M	*						*
191	18 Nov 93	Y	11	2	0	F	*	0	15	1(1)[3]	F	*						*
183	19 Nov 93	Y	1	7		F	*											
189	19 Nov 93	Y	0	16	0	M	*	1	7	5	F	NS	0	16	2	F	*	NS
142	19 Nov 93	N	0	15	0	M	*	0	2	10	M	*						*
210	14 Dec 93	Y	0	16		M	*	20	0		F	*						*
198	17 Dec 93	Y	11	0		M	*											
216	17 Dec 93	Y	2	16		M	*	16=	1		F	*	1=	14		F	*	*
233	7 Feb 94	Y	0	13	0	F	*	10	0	0	M	*	0	0	13	F	*	*

Cont.

Table 3.1 cont.

Nest	Date of Fledging	Final nest	Fledgling A					Fledgling B					Fledgling C					
			Adult			Sex	Sig[1]	Adult			Sex	Sig[1]	Adult			Sex	Sig[1]	BD[2]
			F	Am	Bm			F	Am	Bm			F	Am	Bm			
417	26 Sept 96	N	1	4	3	F	NS											
408	24 Sept 96	N	5=	8		M	NS	1=	10		F	*	2	11		F	*	NS
420	4 Oct 96	N	0	2	11	M	*											
429	11 Oct 96	N	2	9		F	*	11	3		F	*						*
428	14 Oct 96	N	9	2	1	M	*	0	15	0	F	*	0	2	13	F	*	*
439	16 Oct 96	Y	1	10	1	M	*											
446	28 Oct 96	N	0	16		M	*	0	12		M	*	3	9		F	NS	NS
449	1 Nov 96	Y	12	1		M	*	0	12		M	*	0	14		F	*	*
448	2 Nov 96	Y	10	0		M	*											
474	16 Nov 96	Y	1	11		M	*	3	10		M	NS						
462	20 Nov 96	Y	1	16	0	M	*	0	11	1	M	*	0	0	15	F	*	*
466	23 Nov 96	Y	0	9	1	F	*	0	8	1	F	*						NS
476	10 Dec 96	Y	1	18		F	*	2	17		F	*	14	3		F	*	*
493	14 Dec 96	Y	0	14		M	*	7	3		F	NS	10	0		F	*	*
473	18 Dec 96	Y	10	1		M	*											
498	28 Dec 96	Y	10	1		F	*	1	14		F	*	1	9		M	*	*

Cont.

Table 3.1 cont.

Nest	Date of Fledging	Final nest	Fledgling A					Fledgling B					Fledgling C					
			Adult			Sex	Sig[1]	Adult			Sex	Sig[1]	Adult			Sex	Sig[1]	BD[2]
			F	Am	Bm			F	Am	Bm			F	Am	Bm			
513	29 Sept 97	N	1	15		F	*	2	12		F	*						NS
522	16 Oct 97	Y	18	0		M	*	2	13		F	*						*
536	23 Oct 97	Y	0	7	10	M	NS	11	4	0	F	NS						
539	26 Oct 97	N	0	5	12	F	NS	0	10	8	F	NS	0	5	15	F	*	
554	26 Oct 97	Y	0	14	1	M	*	0	13	2	M	*	0	1	15	M	*	*
551	8 Nov 97	Y	0	4	10	M	NS	0[=]	0	18	F	*	0[=]	16	1	F	*	*
550	17 Nov 97	Y	0	12		M	*											
569	3 Dec 97	N	0	14	1	F	*											
575	15 Dec 97	Y	11	0	1	F	*											
577	16 Dec 97	Y	0	13	0	M	*	0	0	16	F	*						*
573	21 Dec 97	Y	7	0		F	*											
578	26 Dec 97	Y	14	0		M	*	0	13		F	*						*
581	27 Dec 97	Y	0	12		M	*	10	0		F	*						*
583	3 Jan 98	Y	12	0	0	F	*	0	0	10	F	*	0	0	10	F	*	*

1. Goodness of fit test to determine wether fledgling fed by a single primary career.
2. Test for brood division applied in broods where at least two fledglings were fed significantly more by one adult. Fledglings in broods of three who were not fed by a single primary career were dropped and the interaction test re-applied. Significant results indicate brood division.
3. A third male fed this fledgling. The number of feeds is in brackets.

Significance levels set at $P<0.05$ for all tests.

Table 3.2. The pattern of parental feeding in different sized broods of white-browed scrubwrens. If one fledgling in a divided brood of three was not fed significantly more by one adult, that brood was classified depending on the other two fledglings. In broods of two where there was no brood division but one adult still fed at least one fledgling significantly more than other adults, that brood was classified as being fed by that adult. Broods of three that did not divide were classified depending on the adult that fed at least two fledglings significantly more than other adults. Anomalies are explained in footnotes. Numbers represent the number of broods. F=female fed offspring, A= alpha male fed offspring, B= beta male fed and G= Gamma male fed offspring.

Brood type	Brood size	Feeding adult								Number of broods
		F	A	B	F/A	F/B	A/B	F/A/B	A/B/G	
Divided	2				8		2			10
	3				6	1	3	3		13
Not Divided	1	5	4	1			1		1	12
	2		5					1[1]		6
	3		3				1[2]			4

1. The female and beta male exclusively fed one fledgling each but the alpha male fed both fledglings

2. Two of the fledglings fed by both the alpha and beta male, while the third was cared for by the beta male.

Table 3.3. Number and percent of offspring that died between census periods during the 1992-1998 breeding seasons. Young only included if complete census records were available. The chi-square test is based on the numbers that survived and died between the three census periods (see text for more details).

Period	Alive at start	Survived	Number died	% died
Fledge - Week 2	712	483	229	32.2
Week 2 - Week 4	483	465	18	3.7
Week 4 - Week 6	465	448	17	3.7
			X^2=260, df=2, p<0.001	

Table 3.4. Survival of young from fledging to week four in different sized broods.

Brood size	No. young fledged (Fl.)	No. alive at Week 2	No. died Fl. – Week 2	% died Fl. – Week 2	No. alive at Week 4	No. died Week 2-4	% died Week 2-4
1	38	28	10	26%	28	0	0%
2	166	120	46	28%	115	5	1.7%
3	501	332	169	34%	321	11	3.3%
Total	705	480	225		464	16	

Table 3.5. A summary of the evidence for and against the functional hypotheses explaining brood division.

Hypotheses	Prediction	Evidence from this study	Prediction supported?
Predation	Brood division and separation should be most pronounced when young are most vulnerable.	Brood division was weakest when young were most vulnerable.	×
Feeding efficiency	Family units should form sub-territories.	Family units did not form sub-territories.	×
	Division should be strongest when young are hardest to find and least mobile.	Young are hardest to find when there is no division.	×
	Division should reduce distance apart between adults and offspring	There was no difference in the distance apart between adults and offspring from family units of one or two fledglings.	×
Sibling competition	Food will be allocated more evenly in divided broods	Variation in weight between young was greater in divided broods.	×
Division by sex	Broods divided by sex	No evidence that adults have a preference for feeding young of a particular sex.	×
Sexual conflict	One sex cares chooses to care for the fledgling requiring the least post-fledgling care.	Males had a weak tendency to feed largest young but there was no evidence that largest young required less care or that males reduced care in other areas.	×
Adult manipulation	Ensures even levels of care by forcing adults to feed fledglings enough for them to survive.	Inequality between parental effort increased.	×

Cont.

Hypotheses	Prediction	Evidence from this study	Prediction supported?
Adult dispersion	Brood division occurs as a result of the breakdown of the pair bond.	Families remain in close proximity throughout the period of parental care.	✗
Fledgling choice	Brood division will form as young become more active in obtaining food	Brood division formed as young became active	✓
	Largest chicks choose to be fed by the best feeder	Largest chicks were predominantly fed by the best feeder	✓
	Fledglings will use aggression to maintain division	Little aggression seen between siblings	✗
	Adults will not use aggression to maintain division	Adults did not use aggression to maintain division	✓
	Adults will feed the nearest offspring	Adults nearly always fed the closest offspring	✓

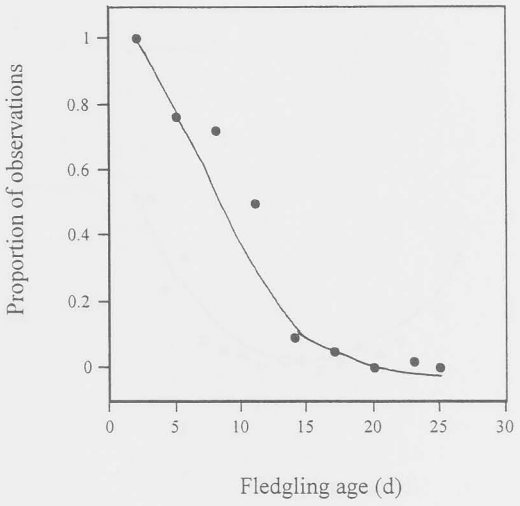

Fig.3.1. Proportion of adult feeds to fledglings during which the fledglings were stationary and within one meter of each other. Points on the figure are calculated from raw data. The line is fitted using a non-linear spline smoother (see results for more details). This analysis was restricted to observations taken within 25 days of young leaving the nest, as older young were never seen stationary and together. The data include 269 observations from 28 broods.

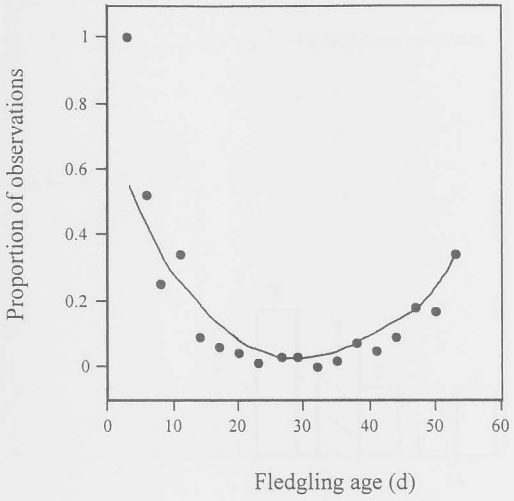

Fig.3.2. Proportion of feeds to fledglings by adults other than their primary carer. Points on the figure are calculated from raw data. The line is fitted using a non-linear spline smoother (see results for more details). Data in this figure come from 879 feeds from 59 fledglings from 24 broods.

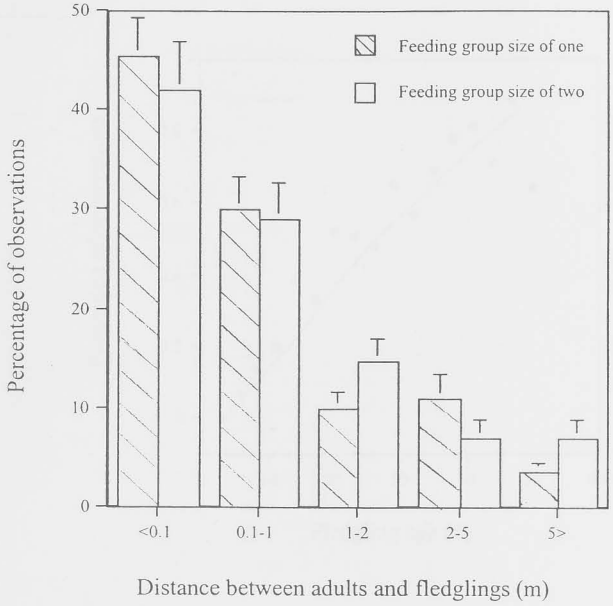

Fig.3.3. The distance between adults and fledglings in feeding groups where an adult only fed one fledgling and where an adult fed two fledglings. Data come from 77 fledglings in 38 broods. Bars represent average percent ($\bar{X}$+SE) of observations for all fledglings.

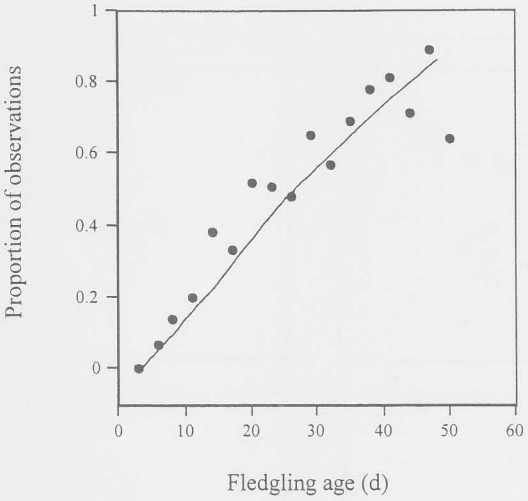

Fig.3.4. Proportion of feeds in which fledglings had an active role in obtaining food from adults. Fledglings were considered to take an active role when they approached or were following the adult immediately before the feed. Points on the figure are calculated from raw data. The line is fitted using a non-linear spline smoother (see text for more details). Data for this analysis come from 1102 observations of 104 fledglings from 51 broods.

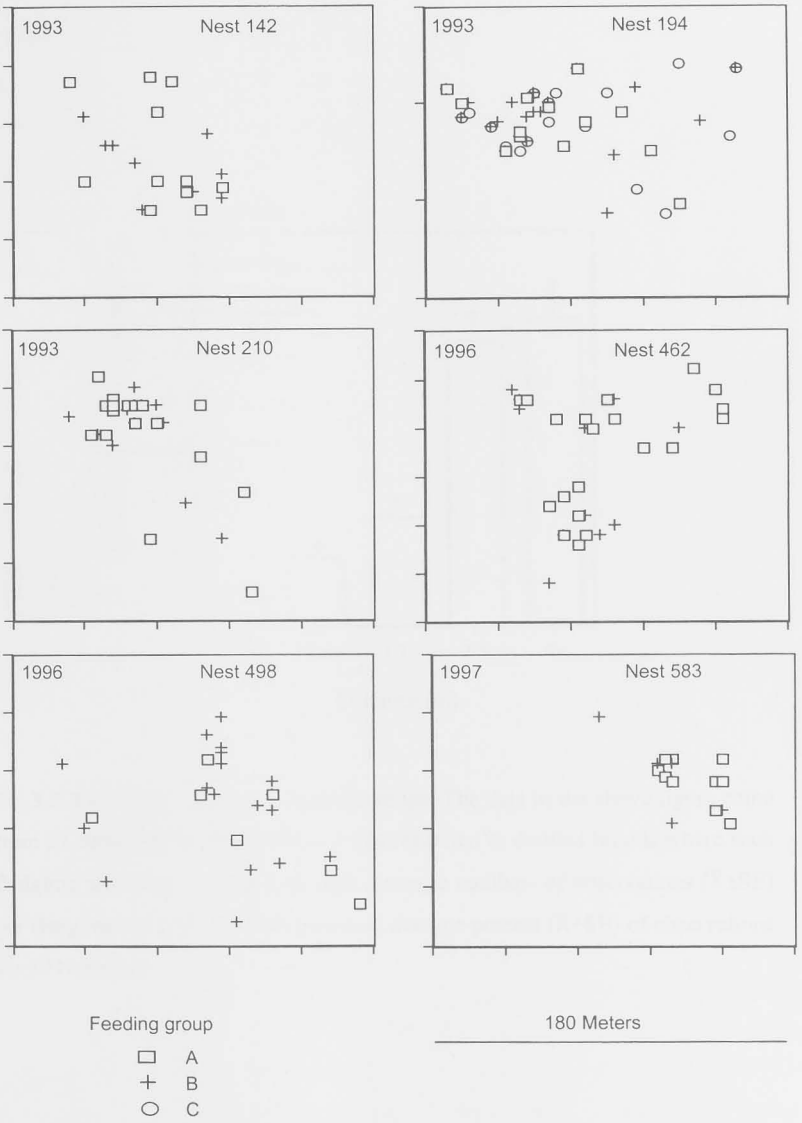

Fig.3.5. Territory use by six randomly chosen divided broods. Symbols represent independent feeds by particular exclusive feeding groups and are taken from the entire dependency period. Non-primary feeds are not included. Discrepancy between number of feeds shown in above figure and those in Table 3.1 due to missing location data.

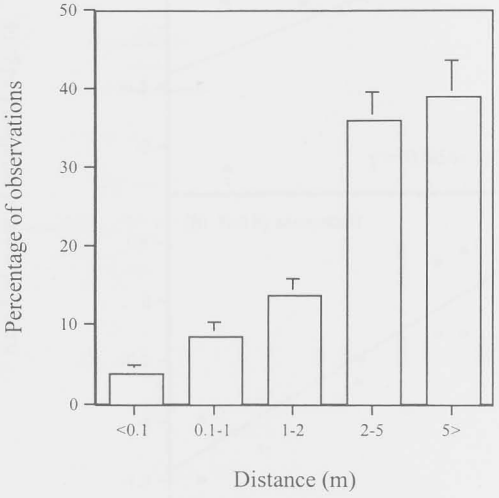

Fig.3.6. The distance between feeding groups. The data in the above figure come from 37 fledglings in 20 broods and was restricted to divided broods where each fledgling was fed by a different adult (average number of observations ($\bar{X}$±SE) per fledgling=11.0±0.57). Bars represent average percent ($\bar{X}$+SE) of observations for all fledglings.

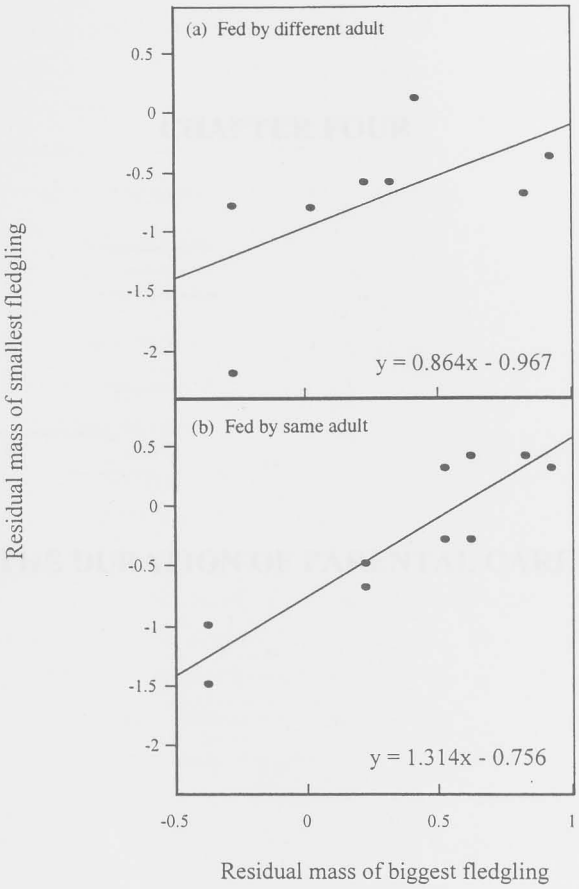

Fig.3.7. The residual mass of the biggest fledgling compared to the smallest fledgling for (a) broods where fledglings were fed by different adults and, (b) broods where fledglings were fed by the same adult. The regression line in figure (a) shows a non-significant relationship between the mass residuals of the largest and smallest offspring (ANOVA: $F_{1,7}=3.2$, $p=0.12$, $R^2adj=0.24$). The regression line in figure (b) shows a significant relationship between the mass residuals of the largest and smallest offspring (ANOVA: $F_{1,9}=40.3$, $p<0.001$, $R^2adj=0.81$).

CHAPTER FOUR

THE DURATION OF PARENTAL CARE

The length of nutritional dependency can be affected by several factors. These factors can be broadly broken down into those which suggest individual fledglings influence the duration of care and those which suggest adults are ultimately in control of the timing of independence (see Chapter One).

There is evidence from several species that fledglings influence the period of dependency. Young spotted flycatchers, *Muscicapa striata*, for example, became independent when the returns from self-foraging were greater than those of begging for food (Davies 1976). This suggests that an individual's foraging ability influences its length of dependence. In white-winged choughs, *Corcorax melanorhamphos*, the pattern between foraging ability and dependency is more complex (Heinsohn 1991). Young choughs switch gradually between begging and self-foraging as returns change. Foraging success improves over time and the amount of food received from adults declines over time, and the variation among birds is thought to be a result of individual differences in ability. These findings suggest that age of dependency is effectively negotiated between adults and offspring. Further, variation among species will occur depending on whether young can pursue a mixed strategy of alternately begging and self-foraging. The difference in termination patterns between spotted flycatchers and choughs may represent such a difference. Because flycatchers mostly take their prey on the wing it may not be profitable to beg and try to forage at the same time, and therefore, young suddenly switch permanently between strategies. Choughs, however, are ground feeders and young could easily alternate between self-foraging and begging as conditions change.

The second hypothesis suggests that adults terminate care at a time that is beneficial to them, and that offspring have little control over this date. Adults may forcibly terminate care if the cost in extending care is greater than the benefit of increased fledgling survival. One example of this might be when adults terminate care of their current brood in order to rapidly renest and thereby increase their overall success by increasing the total number of young hatched per season. Weathers and Sullivan (1989) suggested that this occurred in yellow-eyed juncos, *Junco phaeonotus*, where 42% of young died of starvation in the two weeks after independence. Further evidence along these lines comes from both blackbirds, *Turdus merula* (Edwards 1985), and great tits, *Parus major*

(Verhulst *et al.* 1997), where adults spend less time caring for first broods than they do in caring for final broods. Care to young might also be terminated early if it compromises over-winter survival of adults, either by delaying moult (Evans Ogden & Stutchbury 1996) or reducing adult condition as they head into winter (Svensson & Nilsson 1997). Direct evidence that adults terminate care comes from black-capped chickadees, *Parus atricapillus*, where aggression is used by adults to discourage young from begging (Leonard *et al.* 1990).

Underlying the trade-off and parental termination hypotheses is Trivers' (1974) idea that adults and offspring will disagree over the optimal length of care. He suggested that offspring should demand more food from adults than they are prepared to provide and thus, potentially, extend the duration of care beyond the optimum for adults. Adults, on the other hand, could be expected to terminate parental care before young are fully ready if it compromises their own future reproductive success. Both the duration of care hypotheses are affected by parent-offspring conflict. The trade-off hypothesis suggest that young manage to successfully manipulate adults into providing extended levels of care while the termination hypothesis suggests adults are ultimately in control. In some situations, however, there may be no conflict of interest between adults and offspring. Such situations might occur when young also benefit from early termination of care. For example, in marsh tits, *Parus palustris*, early termination of care leads to early dispersal which increases the offspring's chances of gaining a breeding vacancy (Nilsson & Smith 1985).

Conceptually, the distinction between the trade-off and termination hypotheses is clear; in the former, the length of care is affected by offspring ability, both at self-foraging and manipulating adults into providing food, while in the latter it is due solely to parental control. In practice, however, the hypotheses may be difficult to distinguish. The duration of care may vary because individuals have different foraging abilities or because adults value them differently and so extend care to one but terminate it early to another.

One way of gauging the level of parental control is to investigate the level of intra-brood correlation. If brood members become independent at approximately the same age then it is likely adults are more in control of the duration of dependency than are fledglings, as you would expect young to vary in their foraging ability and their returns from begging. This should remain true

despite the obvious objection that young from the same brood should experience similar conditions and hence make similar choices about when to terminate care. Young from the same brood still potentially compete with each other for food and have different foraging and manipulating abilities. If, however, the level of intra-nest correlation is low, then the picture is less clear. Either adults are preferentially caring for some young longer than others or differences between young from within the same brood are causing the variation. If the intra-nest correlation is low then you might expect to find a correlation between the length of dependency and some characteristic of individual young, such as size, sex or foraging ability.

In this chapter I will investigate factors which may affect the variation in the duration of parental care, both within and between broods. Scrubwrens, *Sericornis frontalis*, unlike species such as marsh tits, are an ideal species to study the termination of parental care because nutritional dependence occurs well before most young leave their natal territory. In birds such as marsh tits this relationship is confounded because young disperse almost immediately after becoming independent (Nilsson & Smith 1985) and so it is difficult to separate factors which effect the timing of dependence from factors that effect the timing of dispersal. In order to assess the relative importance of fledglings in influencing their level of care I will look at individual characteristics of young and their family groups. I will also assess the importance of parental control by looking at the level of intra-brood correlation and whether adults use aggression in order to terminate care.

METHODS

The general methods used in this chapter are described in detail in Chapter Two. The age of nutritional independence was calculated for 49 individuals from 32 broods over three seasons.

Analysis

In order to overcome the unbalanced nature of my data and the within nest replication of siblings, I used a general procedure for estimation (restricted maximum likelihood, REML) of mixed models incorporating random and fixed effects. Nests were fitted as the random effect in the model with the fixed effects being: the number of days from the 1st of September, the sex of the offspring, the number of young surviving to independence within the breeding attempt, the breeding season, whether or not it was the last nest for the season, whether the group had extra-pair males present on the territory during the breeding attempt, whether it was the female's first breeding season, a measure of territory quality, measures of nestling and fledgling mass, the length of time that a young remained on its natal territory after leaving the nest and, where a fledgling was fed significantly more by a particular adult, the sex and rank of that adult. Adult rank was set as either female, alpha male or beta male. Details of how the variables were collected and how the final model was achieved are included in Chapter Two.

The level of intra-nest correlation of fledgling dependency lengths was calculated using the estimated variance components from the final model. Data used in calculating the level of intra-nest correlation were restricted to nests that contained information on two or more fledglings.

In order to assess whether the level of aggression increased near the end of fledgling dependency, I fitted a non-linear spline smoother as described in the general methods section.

RESULTS

Length and determinants of nutritional independence

The length of nutritional dependency varied between 33 and 57 days (Fig. 4.1), with most young becoming independent between 37-53 days. The average gap

between last seeing the fledgling fed and the first time it was seen not being fed was 3.2 ± 0.35 (SE) days.

Female young were cared for, on average, for longer than males (Table 4.1, Fig. 4.2). Using the predicted values obtained from the REML model, the length of female care was 45.5 days, while for males it was 43.7 days. The difference between male and female care is illustrated in Fig. 4.3; in broods which contained both females and males, care of males stopped before care of females in eight out of nine broods (Goodness of fit test: X^2=5.4, df=1, p=0.02). Although males were heavier than females when measured late in the fledgling period (REML analysis: X^2_1=45.8, p=<0.01; predicted weight: females (N=34) 12.9g, males (N=26) 14.5g SED=0.19), there was no effect of either nestling or fledgling mass on length of nutritional dependency (Table 4.1). There was also a weak trend for year to affect the length of care (Table 4.1, Fig. 4.4).

No other effect that I measured approached significance (Table 4.1). There was no relationship between the duration of care and the date within a season that young were born (Table 4.1; Fig. 4.5) or whether it was the final nest for the season or not (Table 4.1; Fig. 4.6). The quality of the territory also did not affect the duration of care (Table 4.1; Fig. 4.7) and nor did the age of the mother (Table 4.1). There was also no relationship between the length of nutritional dependency and the length of natal philopatry for individual young (Table 4. 1; Fig. 4.8). Most fledglings were primarily fed by a particular adult (Chapter Three), which allowed me to test whether the type or sex of the feeding adult affected the duration of care. There was, however, no effect of either sex or rank of the feeding adult on the length of nutritional dependence (Table 4.1).

Variation within broods

Young within a brood had very similar lengths of dependency (Fig. 4.3). I estimated the degree of intra-brood correlation for the length of juvenile dependency by using the variance components of the random model when the fixed model included sex and the random model was the nest. This analysis was restricted to broods where data on the length of dependency were available for more than one fledgling within the brood. The intra-nest correlation using all nests was 0.85 (14 broods).

Brood division did not affect variability in duration of care within broods. In order to examine the effects of brood division on the duration of parental care I repeated the above analysis restricting it to broods that contained two or more fledglings who were exclusively fed by different adults and broods where two or more fledglings were fed by the same adult. In broods in which young were fed by different adults, the intra-nest correlation was 0.82 (n=7 nests; Fig. 4.9a) while in broods where all young were fed by the same adult the intra-nest correlation was 0.85 (n=5 nests; Fig. 4.9b). Data in figure 4.9 are controlled for sex. After controlling for sex, the length of the gap between the earliest and latest young to reach nutritional independence did not differ between the different feeding groups (Wilcoxon rank scores: X^2=0.3, df=1, NS).

The role of aggression

The incidence of aggression increased sharply around day 38 (Fitted spline smoother: $X^2_{2,15}$=91.3; $p<0.001$; Fig 4.10), the time that most young start becoming independent (Fig. 4.1). Although this analysis uses pooled observations, there was no evidence that there was unaccounted for structure within the data (residual mean deviance when a factor two spline smoother fitted = 1.2).

Anecdotal observations also suggest that aggression was used to discourage young from obtaining parental feeds. One example in particular occurred when a female was attempting to renest after a successful first brood. One offspring, still only 35 days old, was seen begging and chasing the alpha and beta males while the males were attempting to allo-feed the female. The result was that the offspring was physically attacked by the alpha male. Although the fledgling remained on the territory for several more weeks it was not seen being fed again nor were there any subsequent aggressive encounters.

Weather conditions

Total rainfall for the months in which adults cared for fledglings (September - February) in 1993 was 300mm, in 1996 it was 375mm while in 1997 it was

190mm. This is compared to the long term average of 352 mm for the same period.

DISCUSSION

Mean duration of care

Juvenile scrubwrens were, on average, dependent on adults for food for approximately 45 days. Although this length of dependency is long compared to many north-temperate passerines (Skutch 1976), it is similar to other species such as the Florida scrub jay, *Aphelocoma coerulescens* (McGowan & Woolfenden 1990), and other members of the family Pardalotidae (Magrath *et al.* 2000). Magrath *et al.* (2000) suggested that Australian passerines might show prolonged periods of care because of the relatively small variation in seasonal food supplies. If food is not abundant when young fledge then they may need to be dependent longer in order to acquire skills necessary for survival. Although many studies have documented the length of parental care for particular species few have tried to explain the variation found among offspring within a species.

Why is the duration of female care longer than the duration of male care?

The only factor to affect the duration of parental care was the sex of the offspring; females were fed for approximately 1.7 days longer than males. Although sex has not been reported to affect the duration of care in other species, this is most likely due to the absence of data during this period rather than sex being unimportant. Further, until recently, most studies could not sex young before dispersal and so were unable to assess the effect of sex on the duration of care.

I suggest three possible explanations of why the length of female care might need to be longer than the length of male care. First, females are smaller than males and so may require extra care; second, females are the dispersive sex and may benefit from extra care; and third, females may take longer to reach

foraging maturity. I believe, however, that none of the above hypotheses explain the difference in the length of care. It is true that females are smaller than males but there was no effect of mass on the length of nutritional dependence; small young were not fed for longer than large young. The second hypothesis, that females being obligate dispersers require extra care, also does not explain the difference between the sexes. There was no relationship between the length of care and the length of natal philopatry, and both males and females remained on their natal territory long after their parents had stopped feeding them, certainly long enough to negate any positive effects of an extra 1.7 days care. The final hypothesis, that females take longer to reach foraging maturity, also does not appear to explain the difference. Most of the variation in dependency times was between broods (Fig. 4.3), with the range between the shortest and longest length of dependency easily swamping the small difference between the sexes. It is hard to see how an extra 1.7 days of care would assist females in gaining vital foraging skills when there is a 19 day difference among broods.

An alternative explanation of the difference in the length of dependency between male and female offspring is that there is an order effect between sexes; in broods where both sexes were present, males stopped being fed before females in eight out nine broods (Fig. 4.3). Two things may be causing this order effect, either a certain sex or rank of adult feeds male offspring and that adult stops feeding before other adults or male offspring choose to terminate care before their female siblings. In white-browed scrubwrens the majority of young were preferentially fed by a single adult, which allowed me to investigate whether the difference in the length of dependency was due to a particular sex or rank of adult stopping care before the others. There was, however, no effect of feeder sex or rank on the duration of care. The remaining explanation is that the offspring themselves influence the duration of care with either male offspring choosing to terminate care early or female offspring choosing to terminate care late. This explanation is also unconvincing as there appears to be no advantage for either sex in early or late termination of care, particularly since the duration of care does not influence the timing of dispersal and hence any advantages gained would be negated by the period of time between the end of care and leaving the territory.

Not only is it unclear why females were fed for longer than males, but it is hard to see how an extra 1.7 days would provide any real advantages to females

considering the relative length of the dependency period. The most likely explanation of the difference in care between the sexes is that there is some sort of within-brood order effect, either due to the offspring or the adults.

Does season or territory quality effect the length of care?

The only other effect that approached significance was the season in which young were born. In scrubwrens, the year with the highest rainfall, 1996, had both the longest breeding season (Magrath *et al.* 2000) and the shortest average period of dependency, which suggests that adults might limit care in good years and extend care in bad years. Food availability has been shown to effect the duration of care in a number of species. In dunnocks, *Prunella modularis*, it was shown that food supplements decreased the length of dependency, suggesting that the amount of food available is important in determining when adults stop feeding (Byle 1990). Verhulst & Hut (1996) found that in broods of great tits, the length of dependency for the second clutch of the season varied between years, with the best year being the shortest. In coots, *Fulica atra*, Amat (1995) found that in the driest year, adults fed chicks more than they did in wetter years. The explanation of this behaviour, which is contrary to the prediction that adults should decrease care when the expected returns are reduced (Amat 1995; Winkler 1987), is that adults are compensating for the lack of available food.

Considering the suggestion that care to young is reduced in good years, it is surprising that territory quality did not affect the length of parental care. Working on the logic that adults extend care in poor years in order to attenuate survival, it may be expected that adults in poor territories would also extend care. Figure 4.7 does show a general decrease in dependency times as territory quality improves, but this result did not approach significance. The failure to find a relationship between territory quality and the length of care may have occurred for two reasons. First, because the measure of territory quality was relatively simple and missed the factors of importance and second, because adults on poor quality territories had to work harder to find food for themselves and so could not afford to extend care to fledglings.

Why doesn't date or nest order affect the length of care?

The order of the nest within the season has been found to affect the length of care in two species, blackbirds (Edwards 1985) and great tits (Verhulst *et al.* 1997). In these species, adults shorten care to the first brood in order to rapidly renest and hence increase the amount of young produced per season. In my study, however, neither the date of fledging or nest order affected the length of care. Scrubwrens are potentially different from blackbirds and great tits in two ways. First, scrubwrens often breed cooperatively. This means that early broods can still be cared for by multiple adults while the female renests. However, there was no significant effect of cooperative breeding on the duration of care. The second difference is that scrubwrens have a relatively long breeding season, up to six months (Magrath *et al.* 2000), compared to around 3 months for many north temperate passerines (Ricklefs 1966). The difference in the length of the breeding season may mean that it is less critical for females to renest rapidly.

Who is in control?

Three lines of evidence from my study suggest that adults are in control of the duration of parental care. First, fledglings from the same brood become dependent at the same time, suggesting that factors that affect the duration of care are common to all offspring within the brood and beyond their influence. Second, when different adults from the same family exclusively fed different young they fed them for similar times, suggesting that the termination of care by one adult might precipitate the termination of care by other adults, and third, the level of aggression peaks around the time of nutritional independence.

Perhaps the key to understanding the factors that drive the length of dependency in the white-browed scrubwren lie in the closeness of termination dates among offspring from within the same brood. This result suggests that the determining factor of the length of dependence operates at the brood level and not at the individual level. Two conclusions can be drawn from this finding. Either the variation between broods is due to territory quality or it is due to parental control.

I was unable to find an explanation for the variation in the duration of dependency found among broods. As previously mentioned, I found no effect of territory quality on the duration of care. I also found no direct evidence that the type of adult influenced the duration of care; the intra-nest correlation and the length of the gap between dependency times was similar for broods where each fledgling was cared for by a different adult and broods where all fledglings were cared for by the same adult. If the type of adult was important in determining duration of care, then fledglings from the same brood who were cared for by a single adult would have a more similar duration of care than those cared for by a different adults. However, there was no difference. Perhaps the factor important in determining the duration of care is not the type or status of the feeding adult but the relative condition of that adult. Since adults were not caught during the breeding season it was not possible to measure relative condition.

One possible explanation for the finding that adults appear to control the length of dependency but still, in divided broods, terminate care at similar times, is that independence of one offspring may precipitate the independence of all young. If, as suggested in Chapter Three, division is a result of young choosing to be fed by a particular adult, then, when its adult terminates care, it might shift its begging efforts to other adults. The costs to individual adults of having to feed extra offspring may be enough to ensure that adults stop feeding young at similar times. In fact, fledglings do tend to swap adults near the termination of care, supporting this idea. Although fledglings can get food from non-focal adults, two lines of evidence suggest that adults are still ultimately in control of the length of dependency. First, it is presumably a reluctance by a particular adult to feed an individual that forces it to obtain food from another adult and, second, young still have similar termination dates suggesting that the final feeding adult stops feeding all young soon after the first adult stops.

Further support for the conclusion that adults are in control of the length of dependency comes from the finding that adult scrubwrens appear to use aggression to terminate care (Fig. 3.10). After five weeks with almost no aggression, there was a rapid increase coinciding with the termination of parental care, suggesting that it was used to encourage offspring to forage independently. The finding that aggression is used to force nutritional independence is similar to the pattern found in black-capped chickadees, where adult aggression peaked

around the time of nutritional independence but before the time that fledglings dispersed (Leonard *et al.* 1990). In scrubwrens, aggression was not seen in every brood, so it is possible that care was terminated in other ways, such as simply refusing to feed young or by avoiding them.

Although in scrubwrens adults appear to control the duration of dependency of young, this is not true in all species, especially those in which young are selected to leave the natal territory quickly. In dippers, *Cinclus cinclus*, the foraging strategy when only a few days old appeared to be the best indicator of length of dependency (Yoerg 1998). Yoerg suggested that one of the possible advantages in becoming dependent earlier was that young could potentially disperse sooner and hence maximise their chances of gaining a breeding vacancy. This was found to be the case with juvenile marsh tits, where offspring were under pressure to leave their natal territory as early as possible in order to maximise their chances of breeding (Nilsson & Smith 1985). Black kites, *Milvus migrans*, are another species where there appears to be little conflict over the date of nutritional independence (Bustamante & Hiraldo 1990; Bustamante 1994). In this species, the end of parental care coincides with the beginning of migration. In species such as marsh tits, dippers and black kites, where the length of nutritional independence is closely tied to the length of natal philopatry, there may be no conflict of interest between adults and offspring over length of dependency, as both maximise their reproductive success by minimising the time that young are cared for. In species such as scrubwrens however, where young remain on the territory after the end of parental care, fledglings should attempt to extend care beyond what adults are willing to provide and adults should retaliate by terminating care before offspring stop demanding food.

Table 4.1. Summary of model fitting the length of nutritional independence. P values for non-significant terms calculated by using change-in-deviance when term dropped from the final model containing sex.

Term dropped	X^2	df	p
Sex of fledgling	4.3	1	0.04
Year	4.3	2	0.11
Nestling mass	2.1	1	0.15
Length of natal philopatry	1.8	1	0.18
Number of siblings	1.0	1	0.32
Group size	0.7	1	0.40
Fledgling mass	0.6	1	0.44
Sex of feeder	0.5	1	0.48
Final nest for season	0.4	1	0.53
Feeder rank	1.0	2	0.61
Female age	0.1	1	0.75
Territory quality	0.4	2	0.82
Date of fledging	0.0	1	1.0

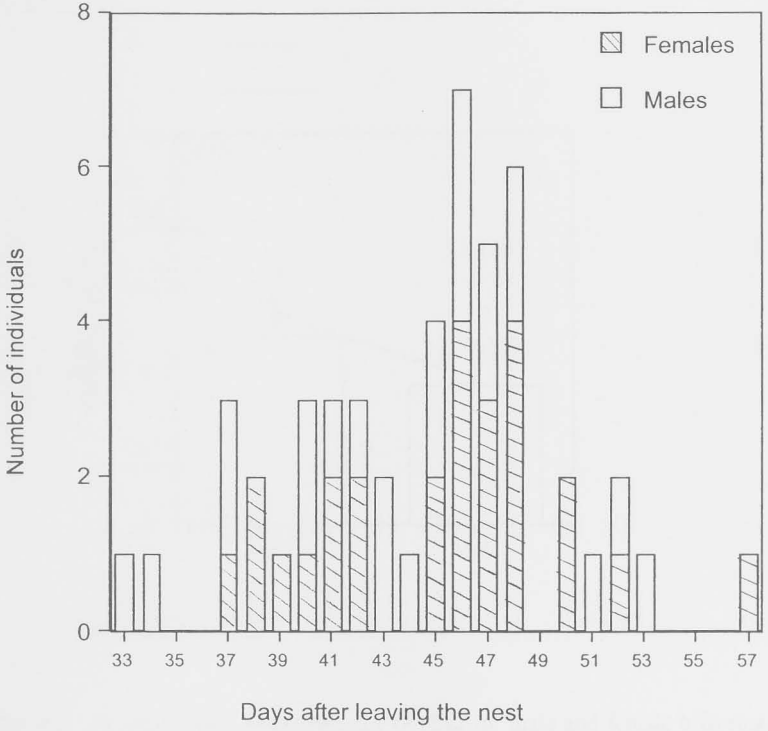

Figure 4.1. The length of nutritional dependence for males and females combined over the 1993, 1996 and 1997 breeding seasons.

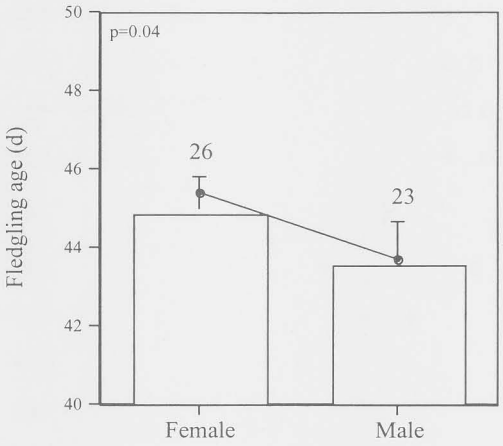

Fig. 4.2. Average length of dependency ($\bar{X}$+SE) for male and female offspring. Sample sizes are given above bars. Also shown are model predictions •, —— . Predictions have standard error of difference (SED) for age of 0.78.

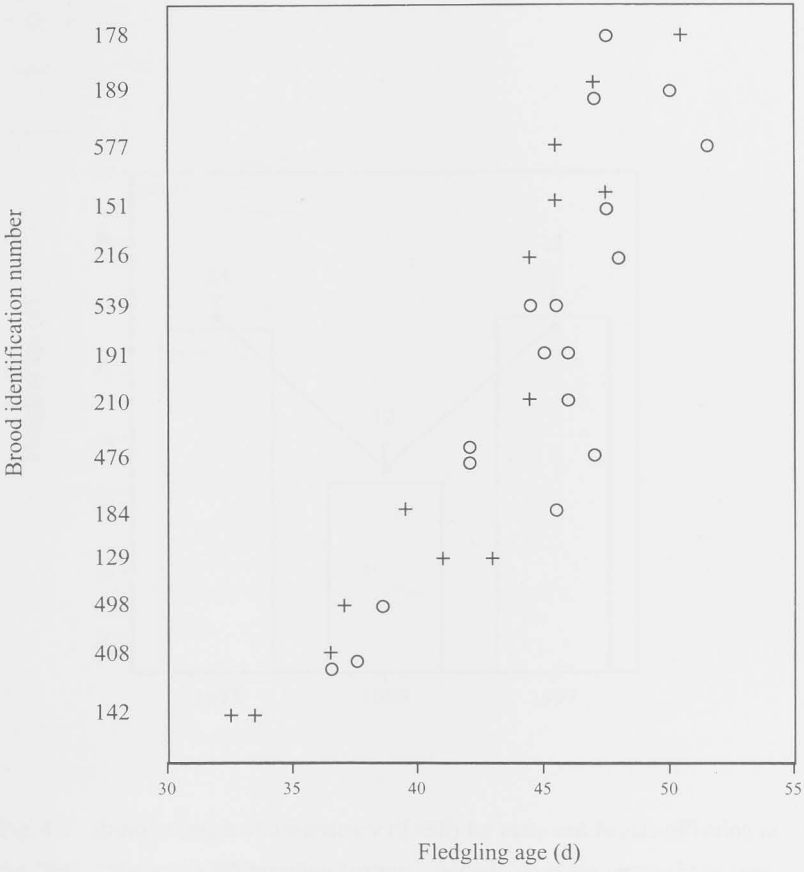

Figure 4.3. The age of nutritional independence for females (O) and males (+) in broods with two or three fledglings combined across years. Broods are ranked according to the average length of dependency in order to highlight the finding that variation between broods is greater than variation within broods.

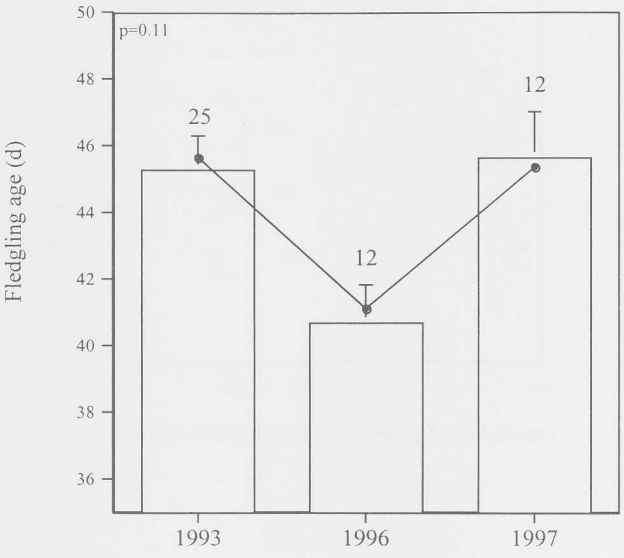

Fig. 4.4. Average length of dependency ($\bar{X}$+SE) for male and female offspring in the 1993, 1996 and 1997 breeding seasons. Sample sizes are given above bars. Also shown are model predictions •, —— . Predictions have standard error of difference (SED) for age of 2.2. Predicted values controlled for sex.

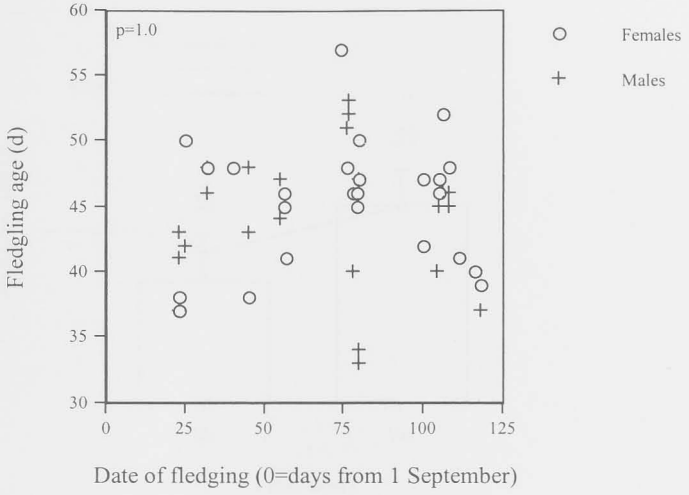

Figure 4.5. The timing of nutritional independence for female and male offspring and the date they left the nest.

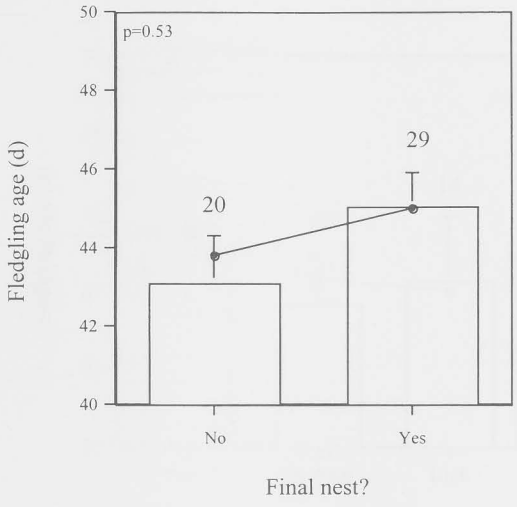

Fig. 4.6. Average length of dependency ($\bar{X}$+SE) for male and female offspring in nests followed by another breeding attempt and nests which were the final breeding attempt for the season. Sample sizes are given above bars. Also shown are model predictions •, —— . Predictions have standard error of difference (SED) for age of 1.89. Predicted values controlled for sex.

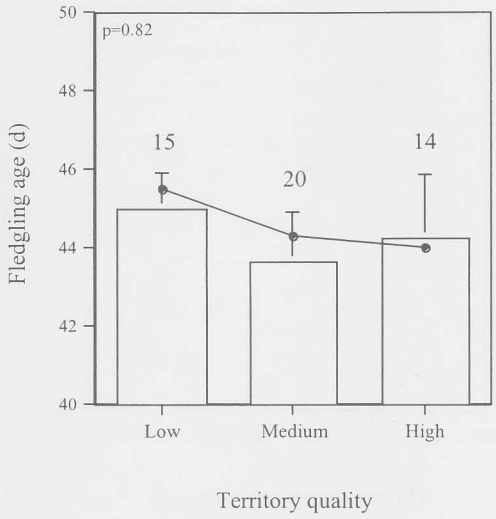

Fig. 4.7. Average length of dependency ($\bar{X}$+SE) for male and female offspring from low, medium and high quality territories. Sample sizes are given above bars. Also shown are model predictions •, —— . Predictions have standard error of difference (SED) for age of 2.4. Predicted values controlled for sex.

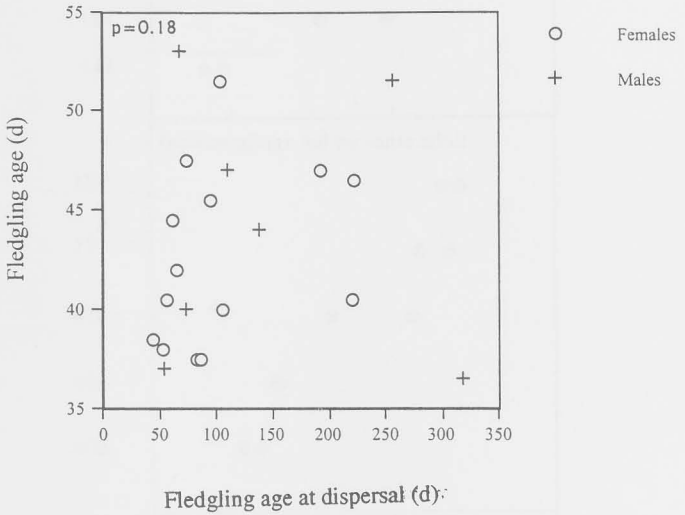

Figure 4.8. The relationship between the length of nutritional dependence and the age when an offspring left its natal territory for males and females.

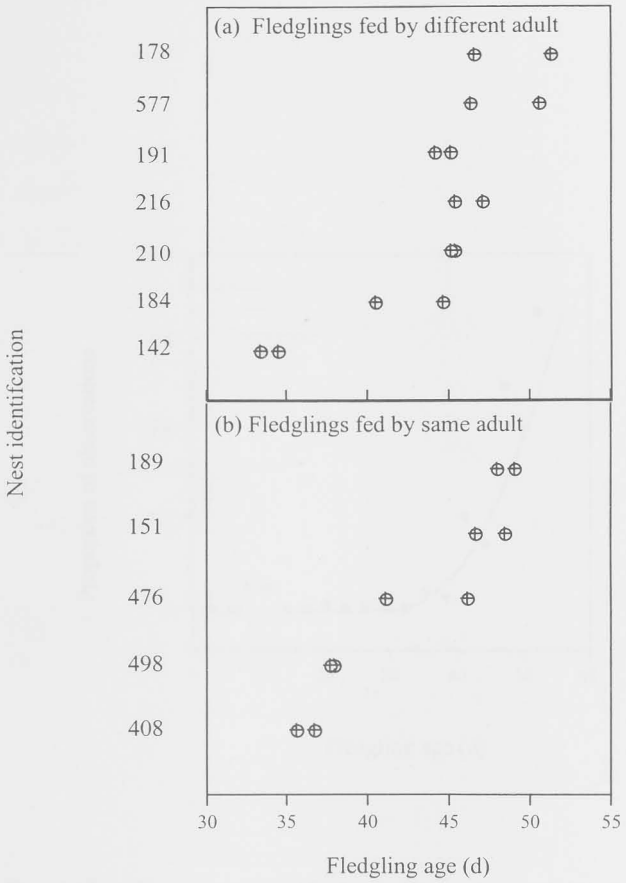

Figure 4.9. The age of nutritional independence for broods where each fledgling was fed by a (a) a different adult and, (b) the same adult. Ages have been controlled for by sex. Broods are ranked according to the average length of dependency in order to highlight the finding that variation between broods is greater than variation within broods.

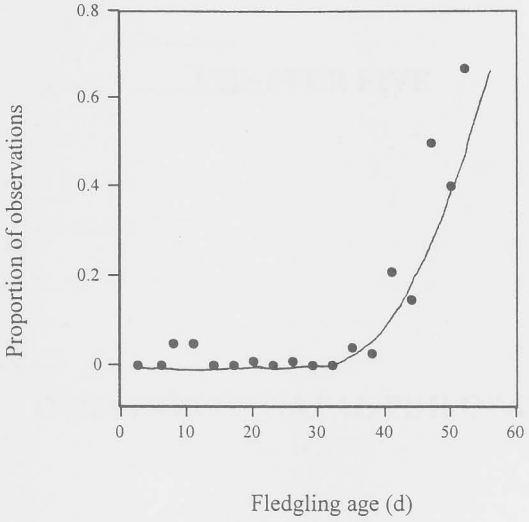

Fig. 4.10. The proportion of observations where adults showed aggressive behaviour towards young. The line is fitted using a non-linear spline smoother (see results for more details). Data in this figure come from 805 interactions from 74 fledglings from 36 broods.

CHAPTER FIVE

DURATION OF NATAL PHILOPATRY

The aim of this chapter is to investigate variation in the timing of dispersal in scrubwrens who leave their natal territory within their first year. At its simplest, young disperse at a time that is either optimal to them or to their parents. The first hypothesis suggests that the timing of dispersal is under fledgling control, while the second suggests that adults eject young from the territory at a time which maximises the adult's own reproductive success.

Evidence that fledglings choose when to disperse to maximise their own reproductive success comes from several species. Large marsh tits, *Parus palustris*, leave their natal territory earlier than their smaller siblings and this increases their chances of obtaining a breeding vacancy in the following season (Nilsson & Smith 1985). Dispersal times also remained the same when adults were replaced with feeding stations, indicating that adults were not forcing young out of their natal territory (Nilsson 1990). Kenward, in a study on goshawks, *Accipiter gentilis*, noted that young were dispersing into periods of peak food availability and suggested that it was potentially advantageous to disperse when food was abundant, as young could then explore potential breeding vacancies while not having to worry about starvation. Like marsh tits, the timing of dispersal in goshawks was not affected when adults were removed and supplementary food was provided (Kenward *et al.* 1993). Fledglings might also delay dispersal in order to wait for breeding vacancies to appear in nearby territories. Pruett-Jones & Lewis (1990) found that that experimentally created breeding vacancies were almost immediately filled by subordinate males.

Evidence that adults force young from their natal breeding group comes from barnacle geese, *Branta leucopsis*, where adults selectively targeted less dominant offspring (Black & Owen 1989). Dispersal may also occur for different reasons depending on the time within the season. Mulder (1985) found that young female fairy-wrens, *Malurus cyaneus*, who dispersed within the season that they were born did so of their own volition while those who waited until the beginning of the following season were forced from the territory by the dominant female.

Understanding which factors influence the timing of dispersal will highlight the reasons why different types of young make different decisions and ultimately help explain how differences among individuals affect their

behavioural options and choices. As in Chapter Four, there are potential difficulties in distinguishing the influence of adults over the ultimate dispersal date. Variation among young can either be explained by differences in attributes of young themselves or differences in the way that adults treat individuals.

Young who remain for the duration of the following breeding season and beyond are excluded from analysis in this chapter. Although this split is somewhat arbitrary, it is necessary for two reasons. First, because the rules used by individuals who delay dispersal are potentially different from those that disperse in their first year and, second, because the causes of natal philopatry and delayed dispersal are beyond the scope of this thesis which primarily focuses on the fledgling period. However, I do include a simple model to determine if, using my restricted data set, any characteristic of offspring helps determine who stays at home beyond their first year.

Scrubwrens, *Sericornis frontalis*, are well suited to studying the timing of dispersal as there are usually at least several weeks between the date that young become nutritionally independent and the date they leave their natal territory. This chapter aims to firstly document the length of natal philopatry and then to examine the factors that may influence its length. Ultimately, the aim of this chapter is to understand the reasons why young leave home when they do and why variation exists among individuals.

METHODS

All female offspring disappeared from their natal territory before or just after the beginning of the next breeding season. Eight out of 25 males, however, remained on their natal territory and were excluded from all analyses regarding the duration of philopatry. As disappearance rates were minimal once young became mobile (see Chapter Three), all disappearances were considered to be genuine dispersal movements. The date of dispersal was estimated for 52 individuals from 29 broods during the 1996 and 1997 breeding season. The general methods used in this chapter are described in detail in the general methods section, Chapter Two.

Recruitment

Young birds were considered to have recruited into the breeding population if, in the following season, they participated in a breeding attempt in which at least one egg was laid. Birds that formed associations with other birds but did not reach the egg-laying stage were not considered to have recruited into the breeding population. Young who remained with their family were considered to have recruited into the population, even though it was unlikely they would be able to reproduce immediately due to incest avoidance (Whittingham *et al.* 1997). However, due to turnover of females, it is likely that they would eventually breed, either on their natal territory with a new female or by dispersing to nearby vacancy.

Adult mortality

The timing of adult mortality was calculated using data collected between 1992-1998. Territories were censused at least once every two weeks during the breeding season (June-February), and the timing of disappearances were recorded as being the mid-point between when the bird was last seen and when the it was confirmed missing. There were no regular censuses during the non-breeding season which, for some territories, extended between February and mid-July, so estimates of the timing of disappearances during this period are less reliable. Only birds who participated in a nesting attempt as part of the dominant pair were included in this analysis in order to ensure that disappearances were due to mortality, as disappearances of subordinate males may be a result of dispersal rather than death.

Analysis

In order to overcome the unbalanced nature of my data and the within nest replication of siblings, I used a general procedure for estimation of mixed models incorporating random and fixed effects. Although the fixed effects varied among models, nest identity was used as the random effect for all models. Continuous dependent variables were analysed using the restricted maximum-likelihood

(REML) procedure while binary dependent variables were analysed using the generalised linear mixed-model (GLMM) procedure (Genstat Committee 1993).

Separate models were used to investigate the length of natal philopatry, the probability that an offspring would disperse early or late in the season, the probability that an offspring would recruit into the study population and the probability that a male would remain on its natal territory during the following breeding season. The fixed effects used to investigate what factors affected the length of natal philopatry and the probability that a young would disperse early or late were: the date that the offspring left the nest (days from the 1st of September), sex, the number of young surviving to independence within the breeding attempt, the breeding season, whether or not it was the last nest for the season, whether the group had subordinate males present on the territory during the breeding attempt, whether it was the female's first breeding season, a measure of territory quality and mass of young at both the nestling and fledgling stage. I used the same fixed effects as in the above models to investigate the probability of recruitment, except that I substituted the dispersal phase, either early or late, for the length of natal philopatry in order to account for the dichotomous nature of dispersal. Finally, the model investigating the probability of natal philopatry was restricted to males and included the same fixed effects as the model used to investigate the length of natal philopatry. Details of the method by which the variables were collected and the final model achieved are included in Chapter Two. The level of intra-nest correlation in the duration of natal philopatry was calculated using the estimated variance components from the final model.

RESULTS

Duration of natal philopatry

On average, females dispersed about two and a half months after leaving the nest in 1996, but five months in 1997; while males dispersed after about five months in each year (Fig.5.1). Statistically, the effects of sex, year and their interaction were significant (Table 5.1). The age at dispersal was not affected by any other

factor, including the date that young left the nest (Table 5.1; Fig. 5.2), or the quality of the natal territory (Table 5.1; Fig 5.3).

There was no tendency for young from the same brood to disperse at the same time. I estimated the degree of intra-nest correlation for the length of natal philopatry by using the variance components of the random model when the fixed model contained sex and season and the interaction effect between the two variables, thus insuring that these factors were controlled for. There was effectively no intra-nest correlation in dispersal times, as the model contained small but negative variance components. Figure 5.4 shows this lack of intra-brood correlation and highlights the finding that the factors which determined the length of natal philopatry acted on individuals rather than on entire broods.

When do young disperse?

Young had a bi-modal pattern of dispersal (Fig. 5.5). Most young that left the territory did so during the summer months of January, February and March and then again at the start of the next breeding season in July (Fig. 5.5a & b). Birds could, therefore, be classified as either early dispersers (before May) or late dispersers (after May). Unlike the results on the length of natal philopatry, neither sex nor season affected the date when an individual left its natal territory, although there was a weak interaction effect (Table 5.2). In 1996, almost all the females had dispersed by May (15/17) while in 1997 only about half had dispersed (10/18; Table 5.3). Males, however, showed no difference in dispersal patterns between years, with 7/12 dispersing early in 1996 while 4/5 dispersed early in 1997 (Table 5.3). There was also no difference in the proportion of males that remained on the natal territory between years, with 3/12 remaining in 1996 while 5/10 remained in 1997 (Fisher exact: P=0.2; Table 5.3).

There was also a weak trend for young with yearling mothers to leave during the early dispersal phase (Table 5.2). Only one fledgling of 11 with a yearling mother remained till the late dispersal phase, while more than half (15/26) of the young with older mothers dispersed during the late phase. The dichotomous classification of early and late dispersal was used in the model investigating who recruited into the study population.

There was evidence that young, before the final dispersal movement, made forays into the surrounding habitat and then returned to their natal territory, as on occasions they were missing in one census but present in the next. Further evidence that young made exploratory forays comes from the observation that some young were also seen away from their natal territory during one observation period but back on their natal territory the next. Only the date of the last observation of a fledgling on its natal territory was used in the above analyses.

Who Recruits?

Young who dispersed from the territory during the late dispersal phase (after May) were more successful at recruiting into the study population (Table 5.4 & 5.5). Sex also affected the probability of recruitment, although only after controlling for the dispersal phase (Table 5.6). Males dispersed later (Fig. 5.1) and recruited at a higher rate (Table 5.6). No other factor tested influenced who recruited into the study population (Table 5.4).

Since there can only ever be one adult female on a breeding territory all 13 females who gained a vacancy, did so as part of the dominant pair. Males, by contrast, can participate in a breeding group as a subordinate male. Of the 14 males that participated in a breeding attempt the year after they were born, none did so as part of the dominant pair; all were subordinate males. Further, of the eight males that recruited from the 1996 and 1997 breeding seasons, six did so because they remained on their natal territory.

It is possible that by restricting the study of recruitment to young who bred within the study population that results might be skewed towards over-representing either early or late dispersers. If one group tended to move further and settle more often outside the study site, then it would be under-represented amongst those recorded as recruiting. This, however, did not appear to be the case. There was no evidence that young from either the early or late dispersal phase moved further (Wilcoxon test: $X^2=1.28$, $N_1=5$, $N_2=9$, df=1, p=0.26). Young from the early dispersal phase moved, on average (SE), approximately 350m (50m) from the nest in which they hatched to the nest in which they first participated in as a breeding adult, while young from the late dispersal phase moved about 235m (78m).

Remaining till the late dispersal phase appears to be the best option for fledglings. It is, therefore, unclear why all young do not delay dispersal. One potential explanation is that competition for resources forces some young to leave early. Territory quality, however, did not affect the timing of dispersal, as might be expected if young were responding to resource shortages. A variation on this idea is that good quality territories contain more individuals than poorer territories and, therefore, young are still forced to leave because of resource shortages. This, however, was also not the case. High quality territories did not contain more group members than low quality territories (Kruskal-Wallis; chi-square=0.05, df=1, p=0.48). Overall means ± SE (n) were: high quality territories 3.3 ± 0.2 (15), poor quality territories 3.0 ± 0.27 (8). Only the last breeding attempt for a particular season was counted for breeding groups that bred more than once, as most young that left did so after the end of breeding.

When does breeder mortality occur?

A potential explanation for the timing of fledgling dispersal is that young are leaving their natal territory in order to fill vacancies created by adults. In order to test this hypothesis I looked at the timing of breeder mortality. Male and female breeder disappearances peaked during the breeding season (August - November) and again during late autumn and early winter (March - May; Fig. 5.6). In contrast to the pattern of breeder mortality, fledging dispersal occurred mainly in the summer months of January, February and March and again at the start of the following breeding season in July (Fig. 5.5 & 5.6). The different patterns of breeder mortality and juvenile dispersal suggests that fledglings do not disperse to fill vacancies left by mortality among breeding adults.

Determinants of natal philopatry for male offspring

During the 1996 and 1997 field seasons eight males out 25 remained on their natal territory until the beginning of the next breeding season. No variable tested significantly affected a fledgling's decision to remain on their natal territory (Table 5.7). This finding, however, should be interpreted with caution due to the small sample sizes.

Weather conditions

Total rainfall for the months in which adults cared for fledglings (September - February) in 1996 was 375 mm, which is just above the long-term yearly average of 352 mm for the same period. The total rainfall for 1997, however, was only 190mm, which is well below the yearly average.

DISCUSSION

The length of natal philopatry was affected both by the sex of the individual and the season in which they were born, with males that dispersed staying longer than females in 1996 but not in 1997. There was also a weak effect of the age of the breeding female on the date that young left their natal territory, with young born into groups with first year females tending to leave during the early dispersal phase. Dispersal mostly took place in two periods, the largest occurring in the summer months in which offspring were born, and then again in mid-winter, just before the beginning of the next breeding season. Before the final dispersal, young birds often made forays into the surrounding habitat and then returned to their natal territory. Similar exploratory forays have been seen in bell minors *Manorina melanophrys* (Clarke & Heathcote 1990), acorn woodpeckers *Melanerpes formicivorus* (Koenig 1981), and jungle babblers *Turdoides striatus* (Gaston 1978). These exploratory forays probably serve to familiarise the individual with the surrounding territories and the breeding opportunities that they might provide.

Who is in control of the date of dispersal?

Three lines of evidence suggest that fledglings, rather than adults, control the date of dispersal in the white-browed scrubwren. First, individual fledglings within a brood left at different dates, suggesting that factors that affect the timing of dispersal operate at the individual rather than the brood level. This finding alone,

however, does not suggest that fledglings are in control, because adults may selectively expel some offspring and not others. However, the finding that date of dispersal was not affected by territory quality or group size, suggests that there is little conflict over access to resources and, therefore, little incentive to expel young before the beginning of the following breeding season. Finally, adults were not aggressive to young after nutritional independence. It is possible that aggression was missed because my sampling effort after the end of nutritional dependency focussed on recording presence and absence only. However, on many occasions I watched young for extended periods of time. In one instance, I repeatedly observed a female early in the breeding season while two female offspring from the previous season remained on the territory. There was no evidence that the dominant female or either of the two males attempted to evict the previous year's young. These findings are similar to those in black-capped chickadees, where aggression peaked around the time of nutritional independence and not during the period when young dispersed (Leonard *et al.* 1990). Further evidence that aggression does not force dispersal in other species comes from marsh tits (Nilsson 1990) and goshawks (Kenward *et al.* 1993), where the length of philopatry did not change when adults were replaced with feeding stations.

Does physical or developmental maturity affect the timing of dispersal?

Studies in some species of bird have suggested that dispersal occurs soon after young have reached a certain level of physical maturity (Simmons 1984; Tyack *et al.* 1998). For example, in red-breasted sparrowhawks, *Accipiter rufiventris*, dispersal occurred after young had fully developed their primary flight feathers (Simmons 1984). This does not explain dispersal in the scrubwren. Siblings from the same brood leave their natal territory at different times, with many broods containing young in which some disperse early while others disperse months later. If dispersal were dependent on reaching a certain level of physical maturity then all young should leave at similar times. Further, there was no relationship between fledgling mass and the duration of philopatry, suggesting that dispersal was not constrained by the need to reach a certain body weight.

A variation on the physical maturity hypothesis is that young need to acquire certain skills before they can disperse (Brown 1987). I did not test this

idea directly, although the bi-modal pattern of dispersal found suggests that this is not the case. If dispersal was based on the acquisition of skills, then it should occur at a constant rate and not be affected by sex unless, of course, both sexes acquired skills at a different rate.

Does the availability of breeding vacancies influence the timing of dispersal?

The availability of breeding vacancies might influence the age when young disperse from their natal territory, with high levels of dispersal coinciding with high breeder vacancy rates. This result is partially supported by evidence from my study. Female dispersal peaks in December and January. This period of dispersal may be driven by the young attempting to fill vacancies left by female mortality during the breeding season. It also peaks again in July, just after the second peak in female mortality and just before the breeding season. Male mortality and dispersal follows similar patterns, although the summer peak in juvenile dispersal is delayed by two months. A potential explanation of this delay in summer dispersal is that males are not as driven by breeder mortality as are females, because male vacancies are most likely filled by older males, and those already present as subordinates on the territory. Further, males almost never become breeders in their first year.

The breeding vacancy hypothesis is contradicted by the similarity in timing of dispersal of juvenile male and female scrubwrens (Table 5.2; Fig. 5.7). Male and female juveniles gain breeding vacancies in different ways and so, under the breeding vacancy hypothesis, would be predicted to have different patterns of dispersal. As there is only ever one female on a territory at any one time, females can only gain a vacancy by replacing other females and yearling females often gain vacancies. Males, on the other hand, have several options. They can remain at home and join their natal group, they can join groups with existing males or they can fill vacancies left by the death or dispersal of a breeder (Magrath & Whittingham 1997; Magrath & Yezerinac 1997; Whittingham *et al.* 1997; Whittingham & Dunn 1998). The last option, that of filling a vacancy left by the death of a breeder, is the least likely to occur, as first year young will generally have to compete with subordinates from territories adjacent to the vacancy. Overall, it seems unlikely that the breeding vacancy hypothesis could

account for the similarity in dispersal patterns of male and female juvenile scrubwrens.

A variation on the hypothesis that young disperse in order to fill a breeding vacancy is that young disperse at a time that maximises their chances of obtaining a vacancy, regardless of adult mortality. Nilsson (1989) found that large marsh tits dispersed earlier and that this ultimately increased their chances of obtaining a breeding vacancy. Screech owls, *Otus kennicotti,* show similar dispersal patterns (Ellsworth & Belthoff 1999), with dominant individuals dispersing earlier than their less dominant siblings. There was, however, no relationship between size and the length of natal philopatry in my study. This is perhaps not surprising. Scrubwrens live in year round territories and in a saturated habitat, with breeding vacancies becoming available as adults die. Other studies, on similar systems, have found that the first to arrive at a vacancy usually obtains that position (Pruett-Jones & Lewis 1990). Assuming this is the case in scrubwrens, then size would not confer an advantage and, therefore, should not affect the age that young leave the territory.

Do young disperse into periods of favourable conditions?

Young might be dispersing into conditions that are the most favourable to survival. One such condition might be an abundance of food (Mulder 1995; Kenward *et al.* 1993), but there is little evidence that young scrubwrens dispersed into an abundance of food. Arthropod abundance in the evergreen forests of temperate south east Australia does not appear to vary much throughout the year (Woinarski & Cullen 1984; Woinarski 1985) and, even if it did, many young disperse in mid-winter, the time in which food availability is likely to be at its lowest.

There is, however, some evidence to suggest that young are dispersing into periods when adult mortality is low. Adult mortality, for both males and females, peaks during autumn and then again during the breeding season (August-December). There is little mortality during summer and winter, the two periods of peak fledgling dispersal. Adult mortality during the breeding season can be explained by the detrimental effects of increased energy expenditure in feeding young and higher levels of predation, particularly of females on the nest.

The second peak in mortality, however, is harder to explain. Adults may be succumbing to the onset of cold weather. If this is the case, then it is likely to affect fledgling mortality as well. This may then explain why young do not disperse during that period. Adult mortality is also low during summer, the other period of peak fledgling dispersal. Again, if conditions are favourable for adults then they are likely to be equally favourable to dispersing young. This pattern may indicate that young are timing their dispersal to coincide with favourable conditions, favourable conditions being a combination of climate and food availability. This would explain why, during 1997, the low rainfall year, less than half of the females had dispersed during the early phase, while in 1996, the good year, nearly all had (15/17).

What determines who recruits into the study population?

Young who dispersed from their natal territory at the beginning of the following breeding season had a greater chance of recruitment into the study population than those who left earlier. It is unlikely that these results are biased by restricting recruitment to young who remained in the study population as there was no evidence that young from either phase went further. This pattern of enhanced success for late dispersing birds is similar to brown thornbills, *Acanthiza pusilla*, where late dispersers were four times more likely to recruit into the population than were early dispersers (Green manuscript in prep.). Further, neither Green's or my study found any evidence that parents forced young to disperse. This finding is something of a paradox, as there appears to be an obvious advantage in delaying dispersal, yet not all young do so. Green suggests that this paradox may be explained by the effects of group size on food availability. Young, who are likely to be poor foragers, must compete with adults for food and, therefore, are forced to disperse when food availability is low. Food supply, however, does not appear to explain why juvenile scrubwrens do not delay dispersal. Firstly, there was no effect of territory quality or group size on the timing of dispersal, which would be expected if dispersal was driven by the need to obtain sufficient food. Secondly, in 1996, the wettest year of the study, young dispersed earlier than in the dry year, which contradicts the limited food supply argument. If young were forced to disperse because of limited food

supplies then, in the good year, young should have delayed dispersal in order to improve their chances of gaining a vacancy.

Not only is it is unclear why more young do not delay dispersal, it is also unclear why late dispersal itself is advantageous. It could be argued that young who remain at home longer are more likely to disperse directly into a vacancy when one occurs nearby. However, there is no evidence that there are more vacancies available during the late dispersal period. Another possibility is that late dispersers are more familiar with their surroundings and, therefore, are more successful when they finally disperse. There is good anecdotal evidence in my study, and several others (Gaston 1978; Koenig 1981; Clarke & Heathcote 1990), that before young finally disperse they make forays into surrounding habitat and then return to their natal territory. However, it is unclear how this ultimately helps them disperse successfully. Presumably, if young find a vacancy on one of these forays, they will not return to their natal territory. This could result in early dispersers being more rather than less successful.

Another possible reason why late dispersers are more successful at recruiting is that many early dispersers simply die before they can return to their natal territory, either through starvation or predation, during one of these dispersal forays. Predation rates on dispersing young are likely to be very high. During the winter of 1996, all surrounding available habitat was extensively surveyed for past dispersers and only 16 banded individuals were found, of which nine were female and seven were male (unpubl. data). Therefore, those that survive to the late dispersal phase are those that have successfully avoided predation and have gained valuable survival experience. Late dispersers are more successful simply by the virtue that they are better survivors than early dispersers. This could also explain why more young do not delay dispersal; if they die during an early foray then delayed dispersal is obviously not an option.

A logical progression from the idea that predation during dispersal forays explains the pattern of recruitment, is that young are not actually dispersing at all but rather are being killed on their natal territory. This leads to the same conclusion as above: that is that young who are recruiting into the study population are simply those that have successfully survived the first year of their life. This last suggestion is, perhaps, unlikely. First, predation levels of young are relatively low once fledglings become mobile, and second, it would be difficult to

explain why depredation patterns varied between sex and season. However, because predation events are very rarely seen it is not possible to deny this idea.

What determines who stays home?

No variable that I tested affected the probability that a male would remain on its natal territory during the following breeding season. This result is surprising as 6 out 8 males who recruited into the study population from the 1996 and 1997 breeding seasons did so by remaining on their natal territory. Further, there is good evidence from other species that delayed dispersal increases an individual's fitness, either through increased overwinter survival or by obtaining a superior breeding position (Eden 1987a & 1987b; Strikland 1990; Ekman *et al.* 1999). If it is advantageous to remain at home then a link might be found between size and philopatry. It is unclear, however, which way this relationship might work. Evidence from magpies, *Pica pica* (Eden 1987a & 1987b), and grey jays, *Perisoreus canadensis* (Strickland 1990), suggests that it is mostly the dominant individual that remains at home, indicating that fledgling mass might affect an offspring's dispersal choice. Alternately, there is evidence in Florida scrubjays, *Aphelocoma coerulescens,* that the least dominant individuals remained on their natal territory, presumably because they would have less chance of obtaining a vacancy than their more dominant siblings (Woolfenden & Fitzpatrick 1990). One possible explanation of the failure to find a relationship between size and the probability of remaining at home is that size might be a poor indicator of dominance, as has been found in song sparrows, *Melospiza melodia*, and white-throated sparrows, *Zonotrichia albicollis* (Wagner & Gauthreaux 1990). However, it is unlikely that this is the full explanation of the failure to find a relationship between size and natal philopatry in scrubwrens as nine males who were the sole male offspring still dispersed. Territory quality has also been suggested to affect the dispersal decision of juvenile offspring (Komdeur 1992). Komdeur (1992) found that Seychelles warblers, *Acrocephalus sechellensis*, from low quality territories maximised their reproductive success by dispersing, while young from high quality territories maximised their success by remaining at home. Territory quality, however, also did not affect the dispersal decision in scrubwrens.

Conclusion

The evidence from my study suggests that dispersal in the scrubwren is initiated by the offspring and that the different sexes pursue different strategies. Young are most likely to be timing their dispersal to coincide with favourable conditions, rather than dispersing into periods when adult vacancies are high. Two lines of evidence support this conclusion. First, the two dispersal peaks for juvenile offspring coincide with the periods of low adult mortality, and second, male and female offspring are likely to use different strategies to recruit into the population yet both disperse at similar times. Two questions from this study remain unanswered. First, why do not all young delay dispersal and, second why do not all males remain philopatric. A possible answer to these questions is that young are being preyed upon, either at home or during dispersal forays, which distorts the observed dispersal pattern. Testing this hypothesis would be extremely difficult as predation is rarely observed.

Table 5.1. Summary of model fitting the length of natal philopatry for 1996 & 1997 field seasons. P values for non-significant terms calculated by using change-in-deviance when term dropped from the final model containing sex and year and their interaction.

Term dropped	X^2	df	p
Sex	5.9	1	0.02
Year	5.2	1	0.02
Year.Sex	4.0	1	0.04
Female age	2.0	1	0.16
Final nest for the season	1.0	1	0.32
Fledgling mass	1.0	1	0.32
Number of siblings	0.8	1	0.37
Date of fledgling	0.2	1	0.65
Territory quality	0.7	2	0.70
Group size	0.1	1	0.75
Nestling mass	0.0	1	1.0

Table 5.2. Summary of model predicting whether an offspring dispersed early (before May) or late (after May) in the 1996 & 1997 field seasons. Significance levels estimated from the Walds statistic. As no term was significant (<0.05) the Walds statistic was calculated by running the model with a single term.

Term dropped	X^2	df	p
Year	1.3	1	0.25
Sex	0.3	1	0.58
Sex.Year	3.4	1	0.07
Female age	3.4	1	0.07
Date of fledgling	2.0	1	0.16
Territory quality	1.4	2	0.24
Nestling mass	1.4	1	0.24
Number of siblings	1.1	1	0.29
Group size	0.1	1	0.75
Final nest	0.0	1	1.0
Fledgling mass	0.0	1	1.0

Table 5.3. Summary of the timing of dispersal for males and females for the 1996 & 1997 breeding seasons.

Year	Condition	Female dispersal		Male dispersal		Male philopatry
		Early	Late	Early	Late	
1996	Wet	15	2	7	5	3
1997	Dry	10	8	4	1	5
Totals		25	10	11	6	8

Table 5.4. Summary of model fitting the probability of recruitment into the study population. Significance levels estimated from Walds statistic when terms dropped from the final model, which included dispersal phase and sex.

Term dropped	X^2	df	p
Dispersal phase	3.9	1	0.05
Sex	4.6	1	0.03
Dispersal phase.Sex	0.4	1	0.4
Nest order	0.4	1	0.40
Fledgling mass	0.4	1	0.52
Nestling mass	0.2	1	0.65
Date of fledgling	0.2	1	0.65
Territory quality	0.2	2	0.65
Group size	0.1	1	0.75
Year	0.1	1	0.75
Female age	0.0	1	1.0
Number of siblings	0.0	1	1.0

Table 5.5. The probability of recruitment into the study population depending on whether an offspring dispersed early (before May) or late (after May). Statistics presented in table 5.2.

Recruited	Timing of dispersal	
	Early (%)	Late (%)
Yes	6 (17%)	9 (56%)
No	30 (83%)	7 (44%)
Totals	36	16

Table 5.6. Probability of local recruitment depending on the sex of the individual for the 1993, 1996 and 1997 breeding seasons. Statistics presented in table 5.4.

Recruited	Sex	
	Females (%)	Males (%)
Yes	13 (23%)	16 (39%)
No	44 (77%)	25 (61%)
Totals	57	41

Table 5.7. Summary of model fitting the probability of male natal philopatry. Significance levels estimated from the Walds statistic. As no term was significant (<0.05) the Walds statistic was calculated by running the model with a single term.

Term dropped	X^2	df	p
Year	2.3	1	0.13
Date of fledgling	1.8	1	0.18
Nestling mass	1.8	1	0.18
Subordinate males present	1.5	1	0.22
Final nest for the season	0.7	1	0.4
Female age	0.3	1	0.58
Male siblings present	0.2	1	0.65
Territory quality	0.6	2	0.74
Fledgling mass	0.0	1	1.0

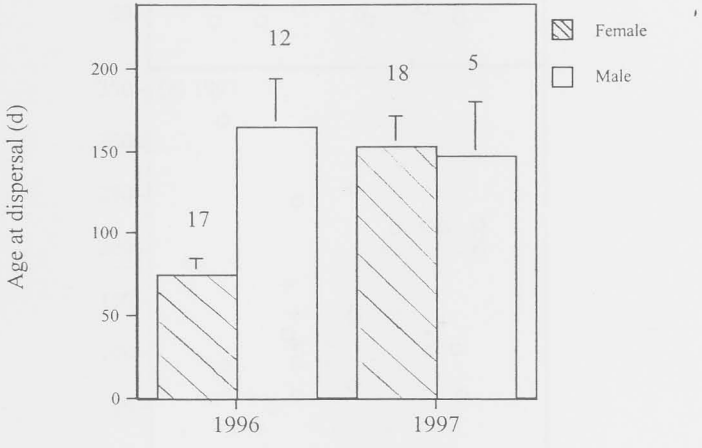

Fig. 5.1 The age at dispersal in days ($\bar{X}\pm SE$) for females and males watched in the 1996 and 1997 breeding seasons. The predictions for the model were: 1996 female 75.1, male 165.5; 1997 female 153.3, male 145.0. The Standard error of the differences (SED) = 31.8. Number of individuals are given over the bars.

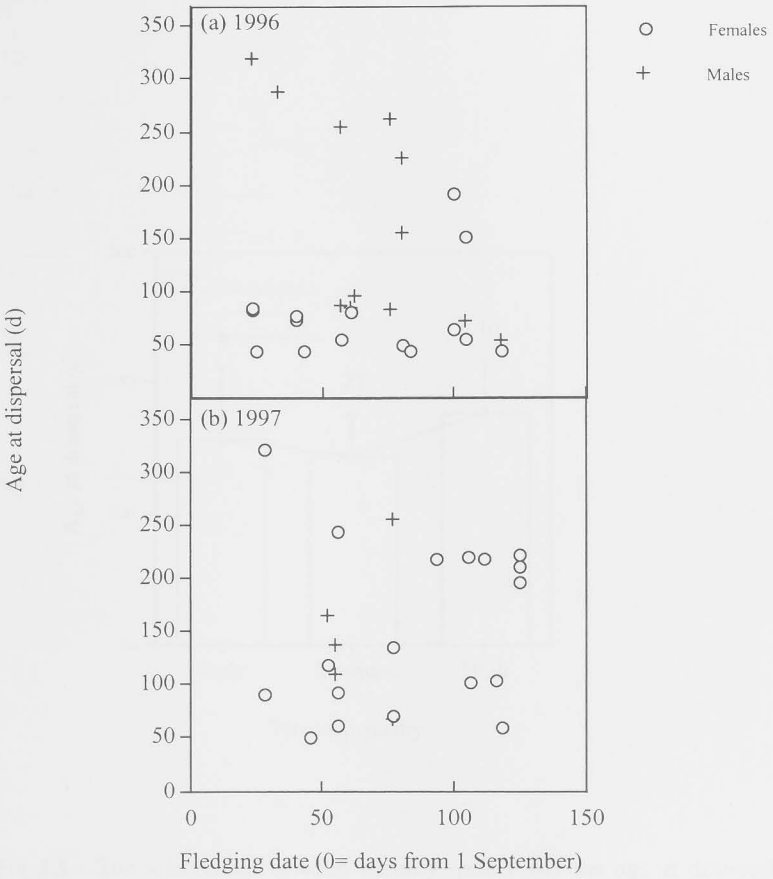

Fig 5.2. Date of fledging and the age at dispersal for females and males watched in the (a) 1996 and, (b) 1997 breeding seasons.

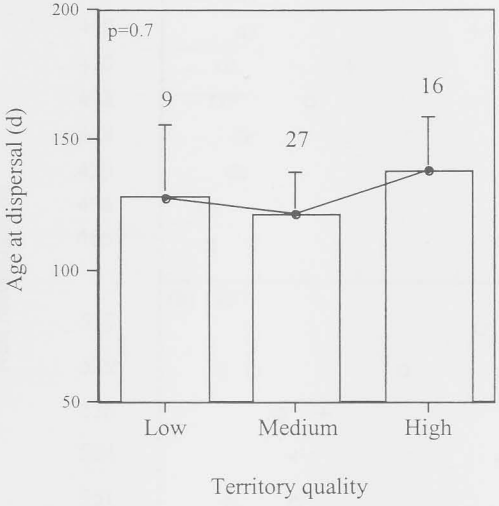

Fig 5.3. The relationship between territory quality and the age at dispersal ($\bar{X}$+SE). Number of individuals given above bars. Also shown are model predictions: • —— The standard error of the differences (SED) = 31.7.

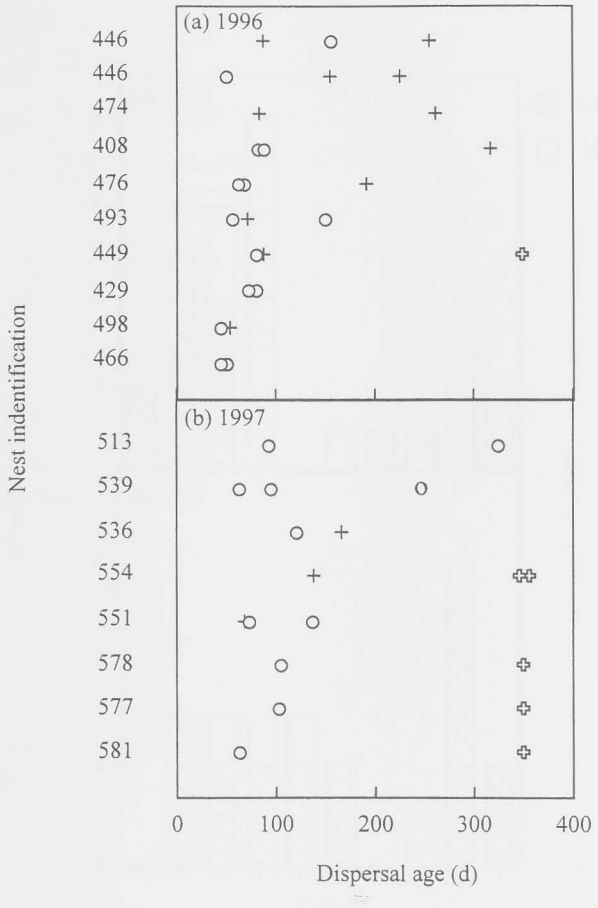

Fig. 5.4. Dispersal age by broods for females (O) and males (+) watched in the (a) 1996 and, (b) 1997 breeding seasons. Non-dispersing males are represented by ✣. Broods which contained a single fledgling were excluded from this figure.

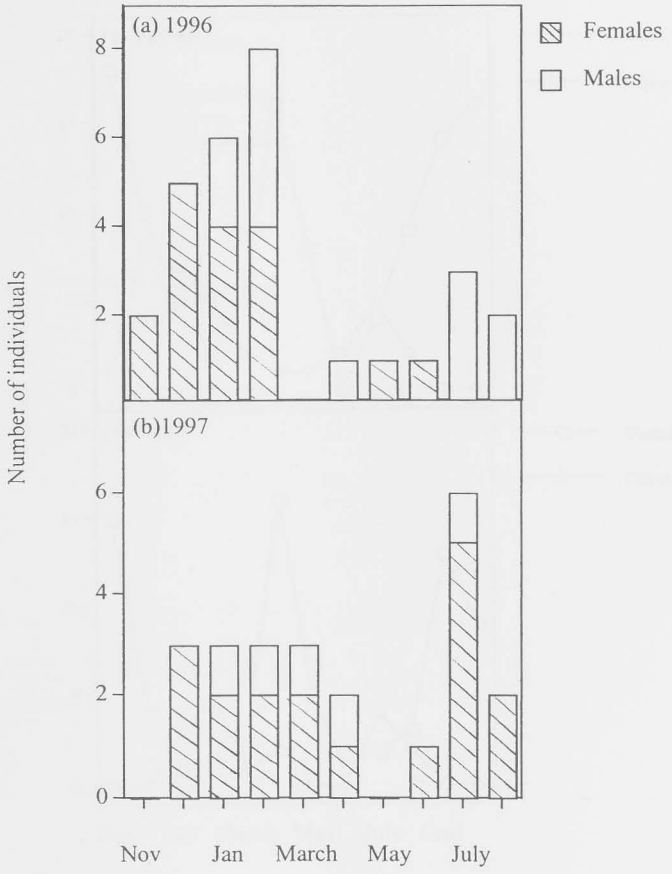

Fig. 5.5. Month of natal dispersal for female and male offspring watched in the (a) 1996 and, (b) 1997 breeding seasons.

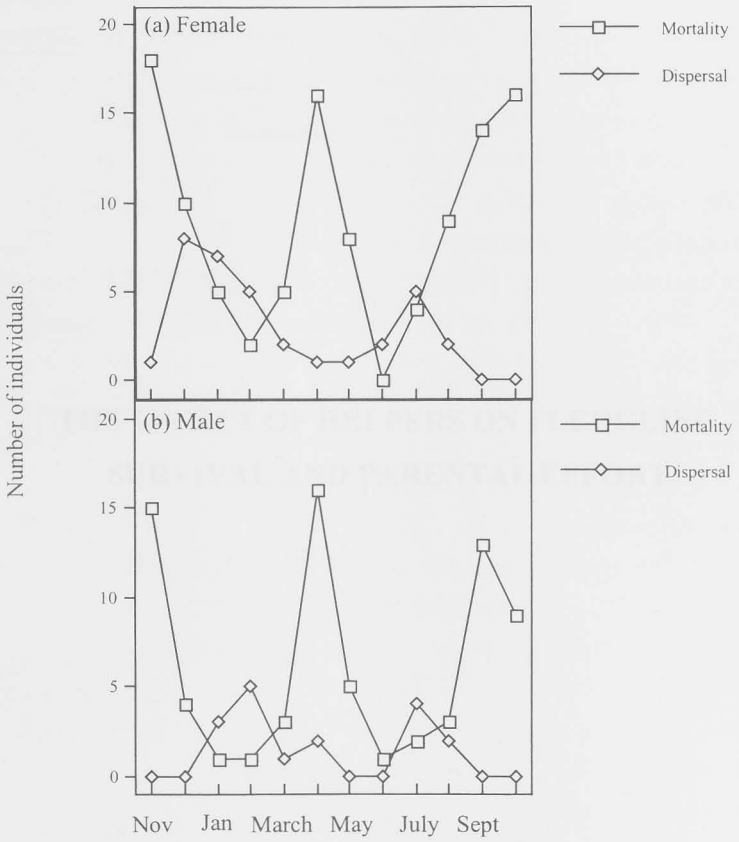

Fig. 5.6. Combined mortality (1992-1997) for dominant pair (a) females and, (b) males and combined dispersal dates (1996-1997) for (a) female and, (b) male offspring. The period of peak breeding occurred between August and December.

CHAPTER SIX

THE EFFECT OF HELPERS ON FLEDGLING SURVIVAL AND PARENTAL EFFORT

A small percentage of birds breed with assistance of extra-pair help (Brown 1987). Two main benefits to breeding adults are commonly cited for such cooperative breeding. One, that it increases offspring survival (Hatchwell & Davies 1990; Emlen & Wrege 1991; Komdeur 1994), and two, that it allows one or both of the breeding adults to reduce their work rate (Brown *et al.* 1978; Stallcup & Woolfenden 1978; Russell & Rowley 1988). Studies at the nestling stage provide support for both of these hypotheses (Hatchwell 1999; Legge 2000). For example, in white-fronted bee-eaters, *Merops bullockoides*, helpers increase the total amount of food provided to offspring and nestling survival increases accordingly (Emlen & Wrege 1991). In superb fairy-wrens, *Malurus cyaneus*, however, the presence of helpers does not increase total feeding rates to nestlings. Instead, the contribution provided by the dominant pair is reduced and nestling survival remains the same (Dunn *et al.* 1995).

In trying to understand why helping behaviour varies among species, Hatchwell (1999) suggested that extra help should be additive where nestling starvation was high but compensatory when starvation was low. When starvation is high, the extra food will increase reproductive success by reducing starvation rates, and when it is low the dominant pair can reduce care without reducing the amount of food young receive. After reviewing the literature both Hatchwell (1999) and Legge (2000) found broad support for this idea. Neither, however, found that breeder survival increased when the dominant pair reduced their effort in response to helpers. Other studies, such as in splendid fairy-wrens, *Malurus splendens* (Russell & Rowley 1988), and rifleman, *Acanthisitta chloris* (Sherley 1990), have found that breeder survival is increased with helpers, but these studies do not differentiate between the effects of reduced work rates or group size per se (Stallcup & Woolfenden 1978; Sherley 1990).

Hatchwell (1999) also found that females and males often differed in their response to beta male help. The difference was manifest in two ways. First, he found that the relationship between a compensatory reduction in care and low nestling starvation was stronger in females. Second, he found that males tended to exhibit compensatory care when their survival was low whereas females only reduced effort when starvation was rare. He interpreted these findings as males being more concerned about their own survival while females were more

concerned about the survival of the brood, and attributed this difference to males being less certain of paternity.

In some species, however, the link between extra help and either a reduction in parental effort or an increase in reproductive success is less clear. The white-browed scrubwren, *Sericornis frontalis*, is one such species. Magrath and Yezerinac (1997) failed to find any effect of beta male help on either nestling mass or fledgling survival, despite the finding that beta male help increased the total amount of food delivered to the nest. Beta male help also did not reduce the amount of food delivered by the dominant pair and nor did it affect breeder survival. That study, however, excluded groups in which the breeding female was a yearling because of low sample sizes. A later study, which included first year birds, found that beta male help increased reproductive success for yearlings but not older birds, and provided evidence that first year females survive better in groups while older birds survive better in pairs (Magrath in press). However, as in studies on bird behaviour, the data collected were from the nestling stage, and it is possible that the crucial period of beta male help occurs during the fledgling stage. Help at the fledgling stage may be important because care of fledglings can be both more energetically expensive (Weathers & Sullivan 1989) and require higher feeding rates (Moreno 1984; Buitron 1988; McGowan & Woolfenden 1990; Evans-Ogden & Strutchbury 1997).

This chapter aims, first, to determine what factors affect the proportion of care provided by adults to young after they have left the nest, and second, to assess the impact of beta male help during the fledgling stage on breeder work rates and survival, and on overall reproductive success.

METHODS

General methods

Details of the study population and methods used for collecting data are contained in the general methods section (Chapter Two).

Proportion of care by each adult

This chapter focuses on the proportion of parental care provided by females, alpha males and beta males to offspring. Proportion of total food provided to offspring was used as the measure of parental care as it was not possible to collect data on feeding rates after young had left the nest. The proportion of total care contributed by each adult during the fledgling phase was calculated by first calculating the proportion of food it provided to each fledgling and then averaging those totals across the brood. This approach was taken to eliminate any bias that might have occurred through uneven sampling of offspring because, as shown in Chapter Three, adults do not feed all young evenly. Effort during the nestling stage was calculated as a proportion of total nest visits, with feeds where the identity of the adult was unknown being allocated in proportion to known effort. Observation periods where more than half the feeds were unknown were excluded from the analysis. Breeding attempts were classified as early or final depending on whether the female laid another clutch of eggs.

Reproductive performance and success

I used four measures to determine reproductive performance and success: First, the number of days between fledging and the laying of the next egg. Second, the number of breeding attempts per season. Third, the total number of young that survived to fledging per season and fourth, the average number of young who survived to independence per nest. Young were considered to have survived to independence if they were seen alive six weeks after leaving the nest. The interval between breeding attempts was the length in days between young fledging from the early brood and the date the first egg was laid in the subsequent attempt. The number of nests and the number of offspring that survived till week six per season was calculated for individual females, as group composition could vary between nests. The average number of young that survived to week six per nest was calculated for group types (explanation below).

Classification of group type

Not all subordinate males provide food to young (Magrath & Yezerinac 1997), so groups were classified as pairs with helpers and pairs without helpers depending on whether a subordinate male provided food to the breeding attempt. Groups were separately classified at both the nestling and the fledging stage. It was possible for the same group to be classified differently at the nestling and fledgling stage. For example, a subordinate male might feed nestlings but not fledglings.

Statistical analysis

I used a combination of statistical modelling and non-parametric tests to examine parental effort. In order to examine the factors which influenced the proportion of care that adults provided to fledglings I used a general procedure for estimation (restricted maximum likelihood, REML) of mixed models incorporating the identity of the adult as the random effect, and a number of fixed effects. This was done in order to overcome the unbalanced nature of my data, and the replicated use of adults within and between seasons. The fixed effects included in the model were: season in which the young were born, the number of offspring surviving per breeding attempt, whether or not the female was a yearling, whether or not it was the final nesting attempt for the season and whether or not the beta male provided any food to the offspring once they had left the nest. Adults were classified as either the female, the alpha male or the beta male and each run as a separate analysis.

I used social groups as the unit for most other analysis. A social group was defined as a particular dominant pair occurring in a particular group type; that is as a pair with helpers or a pair without helpers. If data were available for more than one breeding attempt for a social group then the mean of that variable was used and the group only contributed one datum to that analysis. If the dominant pair was helped by a different beta male in different years then it was still considered to be the same social group because the 'group type' remained the same. If, however, a dominant pair bred alone in one nesting attempt and then bred with the assistance of a beta male in the next nesting attempt it would

contribute two data points to the analysis. This protocol was followed to avoid pseudo-replication within a group type (as in Magrath & Yezerinac 1997). When looking at seasonal reproductive success I classified groups as pairs with helpers and pair without helpers depending on the whether the subordinate male fed fledglings in the final nesting attempt of the season, as no group bred more than twice within any one year. If no young survived to fledging in the final nest of the season then the group was classified using data from the previous brood.

I obtained feeding frequency data for 45 breeding attempts from 28 females over the three years of this study. Seven females bred twice within the same season while 10 bred in more than one season. No female contributed more than three nesting attempts to the data. I followed ninety four fledglings to independence. In total, I observed 1380 independent feeding observations (Chapter Three). Beta males helped feed fledglings in 22 of the breeding attempts. Sixteen nests were followed by another breeding attempt while the remaining 29 nests were not. All results presented in this chapter are taken from the 45 breeding attempts followed and not from the larger study, unless otherwise specified.

RESULTS

Determinants of parental effort during the fledgling stage

Females provided a lower proportion of care to fledglings when beta males also fed them (X^2_1=11.7, P<0.01; Fig. 6.1a), and more care in final breeding attempts (X^2_1=10.6, P<0.01; Fig. 6.2a). There was no interaction effect between nest order and group type (X^2_1=0.38, p=0.53).

In contrast to females, the presence of helpers did not reduce an alpha male's proportion of effort (X^2_1=0.47, p=0.49; Fig. 6.1b) and nor did alpha males reduce their proportion of care between nesting attempts (X^2_1=1.7, p=0.19; Fig. 6.2b). There was also no interaction effect between nest order and group type (X^2_1=2.4, p=0.12).

The only factor to affect the proportion of effort that a beta male provided to fledglings was the order of the nesting attempt; beta males displayed a trend towards providing a greater proportion of care to fledglings from breeding attempts that were followed by another breeding attempt (X^2_1=3.4, P=0.06; predicted proportion of care: early broods 0.40; final broods 0.26).

The proportion of food provided to fledglings by the feeding adults also changed depending on the number of fledglings that survived to week six within a breeding attempt. Females, after controlling for group type and nesting order, provided a smaller proportion of food to broods with more fledglings (X^2_1=6.7, p=0.01; Fig. 6.3a). Alpha males, by contrast, tended to provide a greater proportion of care to larger broods (X^2_1=3.3, p=0.07; Fig. 6.3b). The proportion of beta male effort did not change depending on the number of young that survived per breeding attempt (X^2_1=0.01, p=0.92).

Comparison of dominant pair effort in cooperative and non-cooperative breeding attempts during the fledgling period

To better understand the decisions made by the dominant pair during the fledgling stage I focussed on the change in the proportion of food provided to fledglings by adults in breeding attempts which were not assisted by a subordinate male and in breeding attempts that were assisted by a subordinate male. The non-parametric tests used to compare the change in the proportion of care by females and alpha males are comparable to the REML model used in the above analysis. The results, however, may differ because the non-parametric methods use averaged proportion scores whereas the modelling procedure uses all data, with replication being controlled for by the random model. This method was used because it was not possible to directly compare adults using the REML modelling procedure, as each adult was run as a separate analysis.

(i) Early breeding attempts

Females reduced their proportion of care to early broods when beta males provided assistance (Mann-Whitney test: Z=2.64, N_1=6, N_2=8, df=1, p=0.01; Fig. 6.4a). There was also a weak trend for alpha males to reduce their proportion of

care when beta males provided assistance (Mann-Whitney test: $Z=1.67$, $N_1=6$, $N_2=8$, $df=1$, $p=0.09$; Fig 6.4a). In pairs without helpers, there was a trend for alpha males to provide a higher proportion of food than females (Sign rank test: $Z=1.89$, $N=6$, $df=1$, $p=0.06$; Fig. 6.4a), while in pairs with helpers, both the alpha and beta male provided a greater proportion of food than the female (Friedman test: $X^2=13$, $N=8$, $df=2$, $p=0.02$; Fig. 6.4a).

(ii) Final breeding attempts

In final broods, the proportion of female care was significantly reduced when the beta male provided some assistance to the breeding attempt (Mann-Whitney test: $Z=2.88$, $N_1=15$, $N_2=13$, $df=1$, $p=0.04$; Fig 6.4b), but the alpha male's proportion of care remained unchanged (Mann-Whitney test: $Z=0.35$, $N_1=15$, $N_2=13$, $df=1$, $p=0.73$; Fig. 6.4b). Males and females provided a similar proportion of effort in both pairs without helpers (Sign rank test: $Z=0.31$, $N=15$, $df=1$, $p=0.75$; Fig. 6.4b), and in pairs with helpers (Friedman test: $X^2=3.4$, $N=13$, $df=2$, $p=0.19$; Fig. 6.4b).

(iii) Combined early and late breeding attempts

When data from early and late nesting efforts were pooled, females significantly reduced their proportion of care when the beta male helped feed (Mann-Whitney test: $Z=3.58$, $N_1=18$, $N_2=16$, $df=1$, $p<0.01$; Fig 6.4c), but the proportion of alpha male care remained unchanged (Mann-Whitney test: $Z=0.5$, $N_1=18$, $N_2=16$, $df=1$, $p=0.61$; Fig. 6.4c). When breeding without helpers, males and females provided a similar proportion of food to the offspring (Sign rank test: $Z=0.38$, $N=18$, $df=1$, $p=0.70$) but when breeding with beta male help, the alpha male provided the most care while the female provided the least (Friedman test: $X^2=12.5$, $N=16$, $df=2$, $p<0.01$; Fig. 6.4c).

Do females opt out of care to young in final broods when beta males provide assistance?

There was a trend for females to provide little or no food to final broods after they had left the nest when beta males provided some assistance to the breeding attempt. Females opted out of care, that is provided one or no feeds to young during the fledgling period, in two out of 16 unassisted breeding attempts, while in assisted attempts they opted out of care in seven out of 13 attempts (Fisher Exact: p= 0.09).

In contrast to the trend for females to opt out of care when beta males provided assistance, alpha males fed young consistently. Alpha males opted out of care in four out of 16 unassisted breeding attempts compared to two out of 13 assisted attempts (Fisher exact: p=0.67).

Early nesting attempts were excluded from the above analysis because females who did not care for young did so in order to re-nest and, therefore, were still contributing to the groups reproductive success.

Do females reduce their proportion of care with beta male assistance during the nestling stage?

The finding that females benefit more than alpha males when beta males provide assistance during the fledging stage suggests similar benefits may occur to females during the nestling stage. I used nestling feeding rate data taken from the same subset of adults used in the above analysis to test this hypothesis.

(i) Early breeding attempts

Both females (Wilcoxon test: X^2=4.8, N_1=5, N_2=8, df=1, p=0.03; Fig. 6.5a) and alpha males (Wilcoxon test: X^2=7.0, N_1=5, N_2=8, df=1, p=0<01; Fig. 6.5a) reduced their proportion of effort when beta males provided assistance. The alpha male and female provided similar levels of effort when feeding in pairs without helpers (Sign rank test: Z=1.13, N=5, df=1, p=0.26; Fig. 6.5a) and, when subordinate males provided assistance, all group members fed at a similar levels (Friedman test: X^2=3.0, N=8, df=2, p=0.22; Fig. 6.5a).

(ii) Final breeding attempts

Both females (Wilcoxon test: X^2=6.2, N_1=11, N_2=15, df=1, p=0.01; Fig. 6.5b) and alpha males (Wilcoxon test: X^2=13.2, N_1=11, N_2=15, df=1, p=0<01; Fig. 6.5b) reduced their proportion of effort when beta males provided assistance. In pairs without helpers, alpha males provided a greater proportion of care to feeding nestlings than did females (Sign rank test: Z=2.09, N=11, df=1, p=0.04; Fig. 6.5b). There was no difference in the proportion of care provided by adults when breeding with the assistance of a beta male (Friedman test: X^2=1.69, N=14, df=2, p=0.43)

(iii) Combined early and final breeding attempts

When data from early and final nests were combined, both females and alpha males reduced their proportion of care when the beta male provided assistance (Wilcoxon tests, females: X^2=8.3, N_1=14, N_2=18, df=1, p=0<01; males: X^2=19.3, N_1=14, N_2=18, df=1, p=0<01; Fig. 6.5c). Alpha males provided a higher proportion of care than females in pairs but a similar proportion to females in groups with helpers (pairs: Sign rank test, Z=2.5, N=14, df=1, p=0.01; groups, Friedman test: X^2=3.5, N=17, df=2, p=0.18; Fig. 6.5c).

Effects of beta male care on reproductive success

I looked at the effects of beta male care on four measures of reproductive performance and success (Table 6.1). The delay to re-nesting for groups where the beta male provided some care to fledglings was significantly shorter than the delay in groups where only the dominant pair provided food to fledglings (Wilcoxon test: X^2=6.3, df=1, N=7, P=0.01; Table 6.1). Beta male care did not, however, increase the total number of nests per season (Wilcoxon test: X^2=0.02, N_1=20, N_2=18, df=1, p=0.9; Table 6.1), the total number of offspring that survived per season (Wilcoxon test: X^2=0.95, N_1=20, N_2=18, df=1, p=0.33; Table 6.1) or the number of young produced per nest (Wilcoxon test: : X^2=0.18, N_1=18, N_2=15, df=1, p=0.67; Table 6.1.).

Recent research by Magrath (in press) found that reproductive success of yearling females is higher in groups than in pairs. Although this was not the case in my study, perhaps due to small sample sizes, the direction of the differences is consistent with Magrath's findings. Both yearlings and older females showed similar levels of seasonal reproductive success when breeding in pairs without helpers (Wilcoxon test: X^2=0.4, df=1, p=0.52) and in pairs with helpers (Wilcoxon test: X^2=0.4, df=1, p=0.50). Overall means ± SE (N) were: yearlings in pairs without helpers 2.0±0.71 (4), yearlings in pairs with helpers 3.0±0.55 (5); older females in pairs without helpers 2.3±0.25 (16), older females in pairs with helpers 2.6±0.43 (13). There was also no difference in reproductive success between yearlings who bred in pairs with and without helpers (Wilcoxon test: X^2=1.0, df=1, p=0.3) or between older females who bred in pairs with and without helpers (Wilcoxon test: X^2=0.1, df=1, p=0.73).

Does beta male help during the fledgling stage increase female survival?

There was no detectable effect of beta male help during the fledgling stage on survival of the female until the following breeding season. Two out of 12 females who bred without the assistance of beta male help died before the next breeding season compared to three out of 11 females who had beta male help (Fisher exact test: p=1.0). Group type was classified either on the basis of the female's final breeding attempt within the study if she bred twice or less or on the group type represented at least twice if she bred three times. No female was sampled more than three times within the three years of this study. Only four females changed group types between breeding attempts; three went from pairs to helper groups and the other went from a helper group to a pair. Ten females who bred more than once within the study did not change group types.

Correlation between beta males that helped at the nest and those who helped feed fledglings

Beta males usually fed fledglings and were consistent in care from the nestling stage to the fledgling stage. Within the subset of families used in this

investigation, beta males fed at 83% of nests where the breeding group contained at least two males. Of those that fed at the nest, 84% were seen to feed fledglings at least once (Table 6.2). Only one of 22 beta males that fed fledglings did not also fed nestlings. This individual was only seen feeding young on two occasions (11% of total feeds seen for that fledgling).

DISCUSSION

Three factors affected the relative proportion of care that females and alpha males provided to fledglings after they had left the nest. First, females reduced their proportion of care to fledglings in both early and late breeding attempts when a subordinate male provided food while alpha males, by contrast, did not vary their proportion of effort when breeding with the assistance of subordinate males, at least in final broods. Second, females provided a greater proportion of care to final broods than early broods, while the proportion of care that alpha males provided to the different breeding attempts did not change. Finally, the proportion of care that alpha males and females provided to offspring varied depending on the number of young that survived to independence; alpha males provided a greater proportion of food to larger broods while females provided a lower proportion of food to larger broods.

In contrast to the finding that females benefited proportionally more than alpha males by beta male help during the fledgling period, both the female and the alpha male reduced their proportion of effort to the nest when a subordinate male fed at the nest. Finally, although beta male help reduced the inter-brood interval it did not increase any measure of reproductive success.

Care of fledglings

In this chapter, work rates are based on the proportion of effort rather than absolute effort. This was done because it was not possible to accurately measure the amount of food delivered to young after they had left the nest. Proportion of effort, however, is not a good measure of absolute effort. If the breeding pair fed

at a constant level, beta male help would reduce the proportion of care of both adults without reducing their total amount of care. However, two pieces of evidence suggest that females did, in fact, also reduce their absolute levels of effort when the beta male provided assistance. First, females and not alpha males tended to opt out of care in final broods. Second, the finding that alpha males provided roughly half the total amount of care in both assisted and non-assisted broods (0.53 in non-assisted broods and 0.48 in assisted broods) suggests that females are reducing their levels of care, relative to the number of fledglings within the brood, in response to beta male help. Indeed, assuming beta males helped at the same rate as females (Fig. 6.4 suggests that they help at least as much as females, if not more), beta male help would have to more than double the total amount of food provided to fledglings in order to ensure that female work rates increased even slightly. To demonstrate this, assume an unassisted pair provided 10 feeds each to their offspring after they had left the nest. If the alpha male was still to provide half the feeds when a beta male helped at equal rates as the female, then to increase female feeds by one, that is to 11, the alpha male would have to provide 22 feeds and total feeds would have to increase to 44. This seems unlikely. If, on the other hand, beta male help only increased total effort by one third, that is his help was fully additive, then female help would decrease by 2.5 feeds. Finally, if beta male assistance was to be fully compensated for, female feeds would drop to five and alpha male feeds would remain unchanged.

The finding that females reduced their levels of care and tended to opt out of care when the breeding attempt was aided by a subordinate male is consistent with Hatchwell's (1999) prediction that females will reduce their level of care when the threat of starvation is rare. Magrath and Yezerinac (1997) found little evidence of starvation at the nest. It is likely, therefore, that starvation is also rare during the fledgling stage, although it is difficult to confirm, as disappearances could be a result of starvation rather than predation.

The most obvious benefit to a female of being able to reduce her amount of work is that it might increase her survival. Beta male help, however, did not increase female survival until the next breeding season in this study or in two other studies on this population (Magrath Yezerinac 1997; Magrath in press). Indeed, only a few studies have shown that beta male help has led to an increase

in female survival (Stallcup & Woolfenden 1978; Russell & Rowley 1988; Sherley 1990), and of those cases where female survival was higher in groups, it was unclear whether this was because of reduced feeding effort or larger group size. For example, in splendid fairy-wrens, 76% of females who bred with helpers survived to breed in the next season, whereas only 55% survived without helpers. No mention, however, was made of the effect of helpers on parental effort (Russell & Rowley 1988). No mention, however, was made of the effect of helpers on parental effort (Russell & Rowley 1988).

There are several reasons why I might not have detected an effect of helpers on female survival. First, females probably breed in a variety of group sizes throughout their life and reduction of work in one year may not have immediate effects on their survival in the next. Second, only females in poor condition might reduce care to the brood and not females in good condition, which would then negate any effects of increased survival. Third, beta male help may have both a negative and a positive effect on a female's survival; negative because beta male assistance allows her to renest more quickly and positive because he allows her to work less in final broods. The combined effect on female survival may then be zero. Finally, although beta male help may reduce the female's proportion of care it may not reduce her absolute levels of care, as the proportion measure is not a direct measure of work rates. However, as previously stated, there is good evidence that female effort did decline when the beta male provided assistance.

It is unclear, however, why alpha males do not reduce their proportion of care, particularly in final broods, when assisted by beta males. In pairs without helpers in early broods, it is understandable that alpha males do most of the work. Similar patterns of care have been found in blackbirds, *Turdus merula* (Edwards 1985), where the male almost exclusively cares for early broods while effort is shared between the male and female in final broods. This pattern of care allows the female to renest rapidly. This would also explain why, when breeding in pairs without helpers in final nests, the male and female provide similar levels of care; the female has no alternate reproductive activity. Further, the finding that the proportion of alpha male effort is reduced in early broods when the beta male provides assistance can be explained by the observation that, in pairs in early

broods, the alpha male provides most of the food. Any assistance by an extra adult, therefore, is likely to reduce the alpha male's proportion of care.

What is more confusing, however, is why alpha males do not reduce their proportion of care in final broods. Alpha males are responsible for about half of the observed feeds to breeding attempts with and without beta male assistance. As stated previously, it is perhaps understandable that alpha males and females provide similar levels of effort when feeding in a pair. However, what is not clear is why it is only the female who reduces her proportion of effort when the beta male provides assistance to final broods. This finding is even more peculiar in light of earlier findings on this study population which suggest that when the beta male provides assistance to a breeding effort, the alpha male has possibly lost paternity (Magrath & Whittingham 1997, Whittingham *et al.* 1997).

In some cooperative breeding species, alpha males disproportionately reduce their feeding effort compared to beta males when a beta males gains some paternity (Davies & Hatchwell 1992; Hartley *et al.* 1995; Dunn & Cockburn 1996). This is best displayed in the dunnocks, *Prunella modularis*, and alpine accentors, *Prunella collaris*, where alpha males have been shown to reduce their effort when extra-pair young are present (Davies & Hatchwell 1992; Hartley *et al.* 1995). Magrath & Whittingham (1997) found that beta male scrubwrens who helped feed young at the nest were more likely to be helping in broods in which they were not related to the female and, therefore, potentially had paternity. Furthermore, DNA fingerprinting showed that the beta male fathered 32% of offspring in 53% of broods when unrelated to the female (Whittingham *et al* 1997; Whittingham & Dunn 1998). In the sub-sample of broods used in my study, 72% of beta males who fed fledglings were not related to the group female, suggesting that they might have gained some paternity.

In some species of birds with bi-parental care, any reduction in male help affects survival of the offspring (see Bart & Tornes 1989 & Gowaty 1996 for reviews). Under these circumstances, it is not surprising that males do not reduce their parental effort despite the loss of paternity within the brood; any reduction in care would result in the loss of their own offspring as well as those fathered by the other males. But the option to reduce care exists in species where two or more males gain paternity and where both feed the offspring. Alpha males in my study differ from those of dunnocks and alpine accentors in that they always gain

some paternity within the brood (Davies *et al.* 1992; Hartley *et al.* 1995; Whittingham & Dunn 1998). If they work to a simple rule of thumb to always feed offspring if they have gained any copulations, then this may explain why their proportion of feeds does not change in final broods regardless of their potential level of paternity (Whittingham & Dunn 1998). If this proposition is true, then it is curious why females reduce their proportion of care when beta males help as they alone are related to all offspring.

The second reason why alpha males may not reduce care in final broods when the beta male provides assistance is that, unlike early broods where alpha males have alternate activities such mate guarding and gaining extra-group copulations, in final broods these options may not be available. If the female is not going to breed again then mate guarding is redundant and late in the season there are fewer females around who are potentially fertile. Scrubwrens also have fairly modest levels of extra-pair paternity which would further reduce the benefits of attempting to sire extra-pair young (Whittingham & Dunn 1998).

A third reason why alpha males may not reduce their proportion of care when beta males help could be related to the long lifespan of scrubwrens and the relative stability of scrubwren groups. The oldest known breeding female in our study population was at least seven years old and only five females out of 38 under observation did not survive to breed in the following season. This stability may allow females to control the level of paternity of alpha males from one season to the next. Alpha males who reduce care in one nest because the beta male obtained some paternity may find that they receive even less paternity on the next reproductive attempt. This would mean that there would be an incentive for all males within the group who copulated with the female to provide high levels of care regardless of their levels of paternity. Providing care to fledglings could then be considered as an investment in future reproductive success. This hypothesis has yet to be tested in scrubwrens.

The finding that alpha males increased their proportion of care as brood size increased, while females decreased their proportion of care, is related to the way in which adults selectively provision offspring (see Chapter Three for more details on selective provisioning). In Chapter Three, I highlighted the finding that most young in my study were exclusively fed by a single adult, a phenomenon know as brood division. In divided broods, that is in broods of two or three

young where at least two offspring were exclusively fed by different adults, alpha males cared for more young than females. This finding is highlighted in broods of three which were divided between the alpha male and the female; in 4/5 of these broods the alpha male cared for two fledglings while the female cared for the remaining fledgling. In the remaining divided broods, alpha males exclusively cared for 11 young while females only cared for eight individuals. Further evidence that alpha males provided more care to larger broods comes from the pattern of care in non-divided broods. Typically, when a brood of two or three young failed to divide it was because the alpha male provided most of the care to young while the female reduced her care to a minimum. Out of the 24 young from broods of two or three fledglings that failed to divide, the alpha male exclusively fed 13 of those young while no individuals were exclusively fed by the female. In contrast to these findings, out of the 10 single fledglings that were exclusively fed by a single adult, the female fed five while the alpha male fed only four. In summary, the greater care of large broods by alpha males was due to them feeding a greater number of young, rather than feeding each young at a greater rate.

Comparison between the proportion of care provided at the nest and the proportion provided after young had left the nest

In contrast to the fledgling period, there is no evidence that alpha males benefited more than females when beta males provided food at the nestling stage. During the nestling period, both alpha males and females reduced the proportion of food they delivered to the nest when beta males provided food, both in early and final nesting attempts. The relative proportion of care provided by the dominant adults in pairs without helpers also changed between the nestling and fledgling periods. In early nesting attempts males and females provided equal care during the nestling period but males provided more care during the fledgling period, while in final nests the pattern was the opposite, males provided a greater proportion of food during the nestling period but an equal proportion during the fledgling period.

The finding that, when beta males helped, alpha males reduced their proportion of care during final breeding attempts at the nestling stage but not at

the fledgling stage is curious. Perhaps, because the nestling period is less than half the length of the fledgling period (Magrath *et al.* 2000), females were willing to provide a greater proportion of food to the nest knowing that they could reduce their effort during the longer and more energetically expensive fledgling period (Weathers & Sullivan 1989). Alternatively, the difference may again be a reflection of the way in which fledglings are generally fed by a single adult rather all feeding adults. If, once the feeding patterns are established, each adult has a designated number of young to feed, then the variance in feeding rates between adults is likely to be greater than if all adults fed all young. Therefore, after fledging, females, rather than feed all young slightly less than the alpha male, drop out of feeding almost entirely. The alpha male is then left to take most of slack left by the female, hence the finding that females provide a higher proportion of care to the nest than they do to fledglings.

The finding that both males and females reduced their proportion of care to the nest when beta males helped is different from that of Magrath and Yezerinac (1997), who found that the total amount of food provided by the dominant pair to the nest did not decline when beta males provided assistance. The major difference between the two studies is that I used the relative proportion of food provided by the different adults, whereas Magrath and Yezerinac used total amounts of food provided. The results, however, are not contradictory. In Magrath and Yezerinac's study, the total proportion of the dominant pairs effort also declines when the beta male provided assistance as, when the beta male did feed, he did so at the same rate as the female but at a lower rate than the alpha male. Also consistent with my study was the finding that alpha males provided more parental care than females overall.

Do beta males actually increase reproductive performance?

In contrast to care by beta males at the fledgling period, Magrath and Yezerinac (1997) could find no effect of care of nestlings by beta males on the inter-nest interval. This is surprising because I found that 84% of beta males that helped during the nestling period also helped care for fledglings. The reason may be that while Magrath and Yezerinac (1997) considered the effects of helping in both successful and unsuccessful nests, I only considered the effects of helping for

nests that raised at least one offspring to independence. Indeed, I was limited to only using successful nests because it was obviously not possible to consider the effects of helping at the fledgling stage on nests that failed to fledge young. By focussing on the entire breeding effort, Magrath and Yezerinac placed increased importance on failed nesting attempts which provide less opportunity for beta males to decrease the inter-nest interval.

Given that beta male care of fledglings reduced the inter-nest interval after successful nests, why didn't this result in more breeding attempts. Perhaps because the 11 day advantage that beta males provided is trivial in a season which can last up to six months and in which, at most, a female can have only 3 successful nests.

The finding that beta male help during the fledgling period did not increase reproductive success is consistent with the findings of Magrath & Yezerinac (1997) that beta male help at the nestling stage also did not increase reproductive success. The obvious reason why beta male help did not increase reproductive success in my study is that they probably did not increase total feeding rates to offspring, as females reduced care when beta males provided assistance.

Although the finding that beta male care during the fledgling period did not increase reproductive success is consistent with Magrath and Yezerinac's (1997) finding, it is not consistent with a later finding that beta male help increased success for yearlings but not older birds (Magrath in press). In my study, yearling reproductive success was also not increased by beta male help. However, care must be taken with that result as sample sizes were small (only nine first years in my sub-sample) and the trend was in the right direction.

Table 6.1. Measures of reproductive performance and success. Medians and range are presented for days to renesting while means and standard errors are shown for the remaining measures. Groups are classified according to whether the beta male provided food to fledglings and averaged where more than one reproductive attempt occurred. See text for more details on measures of reproductive success. Significance measured using Wilcoxon test.

	Pairs	N	Groups	N	p
Days to renesting	26.5 (18-49)	6	15.5 (9-17)	6	<0.01
Number of nests per season	1.5±0.14	20	1.4±0.12	18	0.90
Number of offspring to independence per season	2.3±0.24	20	2.7±0.31	18	0.33
Number independent young per nest	2.1±0.17	18	2.2±0.19	15	0.67

Table 6.2. Pattern of help provided by extra-pair males.

Fed Nestlings	Fed fledglings		Total
	No	Yes	
No	4	1	5
Yes	4	21	25
Total	8	22	30

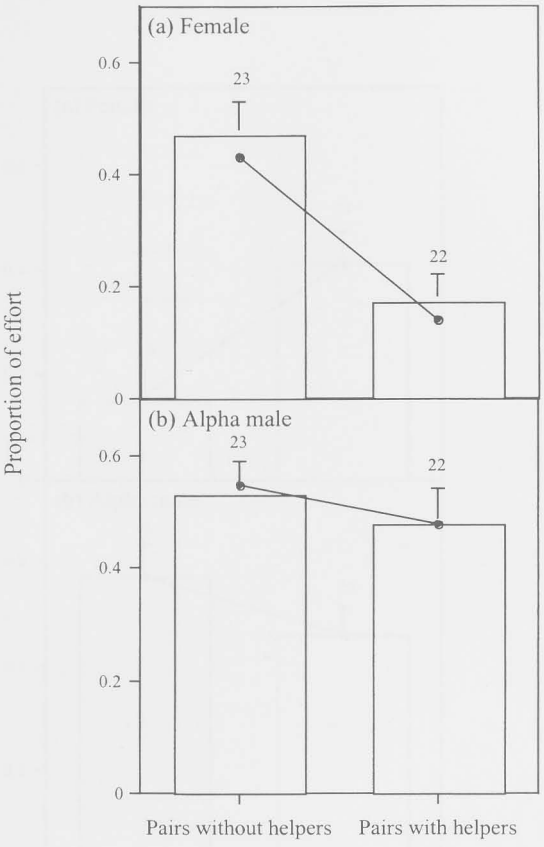

Fig 6.1. The proportion of feeds ($\bar{X}$+SE) to fledglings in pairs without helpers and pairs with helpers by the (a) female and, (b) alpha male. Number of individuals given above bars. Also shown are model predictions: • —— The standard error of the differences (SED) for females was 0.07 while for alpha males it was 0.09.

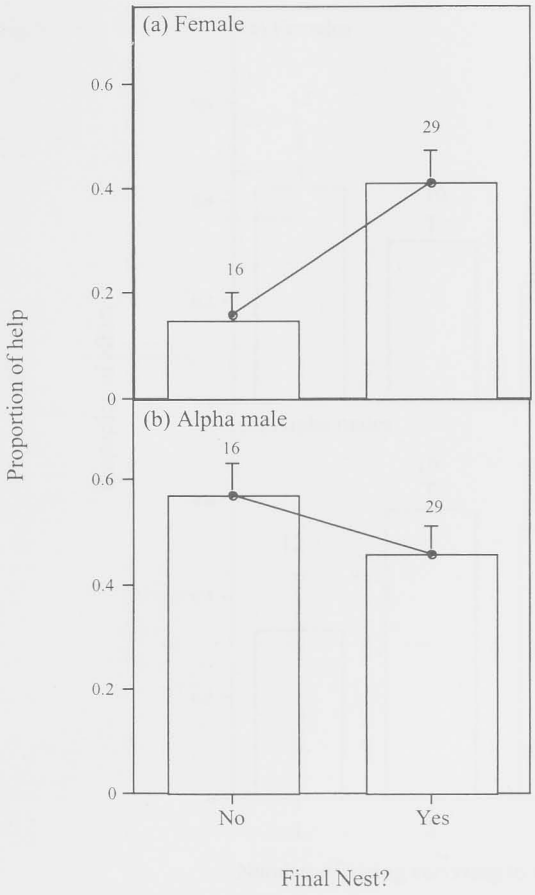

Fig 6.2. The proportion of feeds ($\bar{X}$+SE) to fledglings in early nests and final nests by the (a) female and, (b) alpha male. Number of individuals given above bars. Also shown are model predictions: • —— The standard error of the differences (SED) for females was 0.07 while for alpha males it was 0.09.

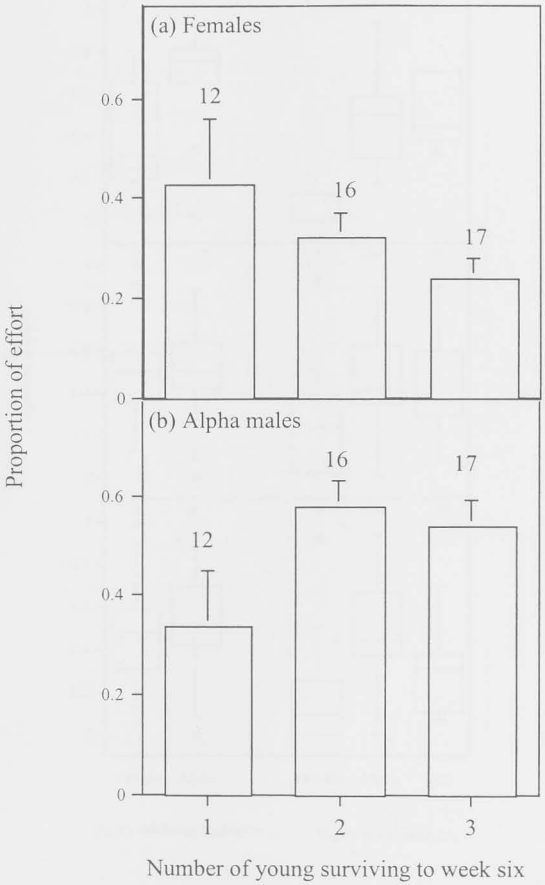

Fig 6.3. The proportion of feeds ($\bar{X}$+SE) to fledglings in broods of different size for (a) the female and, (b) the alpha male. Number of individuals given above bars.

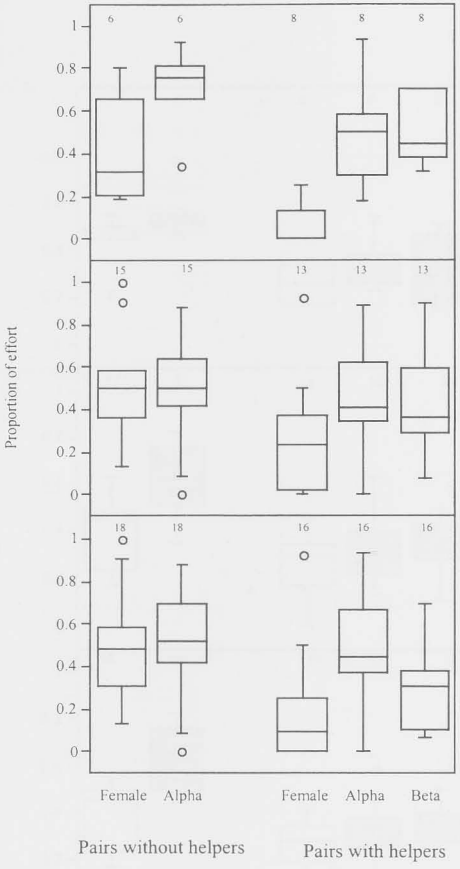

Fig. 6.4. The proportion of feeds brought to fledglings in unassisted pairs and assisted pairs in (a) early broods, (b) final broods and, (c) combined early and late broods. This figure shows boxplots, in which heavy bars indicate medians, boxes indicate interquartile ranges, vertical lines indicate the range of values that lie within 1.5 interquartile ranges of the top and bottom of boxes and o represent more extreme values. The number of broods is given above plots. See text for statistical tests.

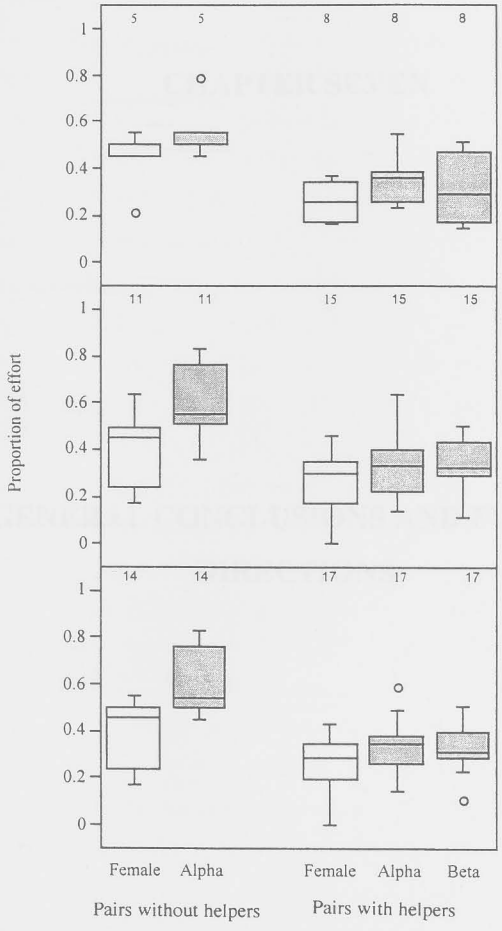

Fig. 6.5. The proportion of feeds brought to nestlings in pairs and groups by adults in (a) early broods, (b) final broods and, (c) combined early and late broods. This figure shows boxplots (see figure 6.3 for full description of box plots). See text for statistical tests.

CHAPTER SEVEN

GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

The four main chapters of this thesis each focus on a different aspect of post-fledging parental care. The focus in each chapter was to look at why events occurred and to place the answer in an evolutionary context. Why are broods of young divided between the feeding adults for the purposes of care? Who controls the length of nutritional dependency and why do young leave their natal territory when they do? Why do feeding adults provide different proportions of food to offspring and why does this change depend on the order of the breeding attempt?

Brood division has been documented many times before and numerous hypotheses have been proposed to explain this behaviour. Previously, however, it was presumed that brood division was a parental strategy designed to maximise adult reproductive success and, as a consequence, hypotheses were proposed to explain how adults might benefit from selectively feeding particular individuals. The first notion that brood division might be a result of fledgling competition came from Slagsvold (1997) who, on finding that largest young were often fed by the best feeder, suggested that competition amongst siblings might explain who feeds whom once a brood has divided but that it did not, in itself, explain why broods divided. The logical progression from this idea is that sibling competition does explain brood division and that adults do not have a strong preference for who they feed.

My results provide compelling evidence for the idea that brood division is a result of sibling competition. Brood division forms as young take an active role in obtaining food from adults. When a feeding adult is removed, its primary fledgling follows the remaining adults about the territory and adults do not try to discourage this behaviour. Further, adults were rarely aggressive towards young and nearly always fed the closest young to them when they found food. Finally, as would be predicted if young picked a particular adult to feed them, largest young were generally fed by the adult that was the best feeder at the nest. My results also dismiss the assumptions of each of the alternate hypotheses.

My research suggests that there are two areas where further study would enhance our understanding of brood division. First, more needs to be known about the mechanisms used to maintain separate feeding groups, particularly in species where families tend to forage in close proximity. Second, studies should attempt to obtain direct evidence that the most dominant individual is maximising

its food intake by its choice of adult. Relating to both of these areas is the peculiar finding that young do not appear to exclude others from their feeding groups. If large young choose to be fed by the best feeder than you might also expect them to keep other young away from that adult. These questions could be approached experimentally. In my study I removed feeding adults for one hour and observed the effects that this had on the collapse of feeding groups. This may not, however, be a long enough period, as although orphans did follow the remaining adult I did not see any orphan get fed. Another approach may be to handicap adults. Best feeders could be handicapped in the latter part of the nestling period to see if the largest young still choose to be fed by them.

Very little research has been carried out which looks at factors which affect both the length of the fledgling dependency period and the length of natal philopatry. The end point of both of these periods can be examined in the context of parent-offspring conflict theory (Trivers 1974). Young and adults are suggested to disagree over the length of parental care because, although each is related to each other they are, ultimately, more concerned about their own welfare. The question then becomes who is more in control of the length of these periods and why do they vary among individuals.

In my study there was little variation in the length of dependency among young from the same brood, suggesting that factors that affected the length of dependency operated on broods rather than individuals. This finding suggests that adults are in control of dependency. Further, the end of dependency coincided with an increase in parental aggression suggesting that adults encouraged young to stop begging before the time that they would have chosen to do so. Evidence from my study also suggests that the termination of care by one adult precipitates the termination of care by the others, perhaps because of the increased cost of feeding more offspring. Other studies have shown that adults use aggression to terminate care (e.g., Leonard *et al.* 1990), but no other study has shown that this also coincides with high levels of intra-brood correlation in dependency times or that an adult's decision to terminate care is dependent on the activity of other adults.

To better determine who is in control of the length of dependency, it would be useful to have information on the actual returns from begging and the returns from self-foraging, particularly around the period leading to the

termination of care. If, as I suggest, parents determine the length of fledgling dependency, then there should be a period when young attempt to obtain food from adults but adults refuse to feed young. The remaining question that I failed to answer was what factors determined the mean length of dependency of individual broods? The most obvious answer is that different broods became independent depending on the quality of their natal territory. This, however, was not the case, at least with the territory quality index that I used. Perhaps a better index of territory quality is needed.

Unlike the termination of parental care, young appear to choose when they leave their natal territory. The most likely overall explanation of timing of natal dispersal is that young leave when conditions are most favourable, as indicated by the finding that the peak dispersal periods coincide with the periods of low breeder mortality. Further evidence that young chose to leave is that there was little intra-nest correlation in dispersal times; young from the same brood left at different times. It is possible that adults selectively expelled certain individuals before others, but there was little evidence that aggression, either by siblings or adults, forced dispersal. There was also no evidence that territory quality or group size affected dispersal timing, which would be expected if adults needed to expel young due to resource constraints.

More difficult to explain is the finding that young who dispersed late maximised their chances of recruiting into the breeding population. If there were no constraints on dispersal and late dispersal improved the probability of recruitment then all young should delay dispersal. Perhaps young were forced from their natal territory, although it is difficult to explain why. If late dispersal maximised the probability of recruitment then it would be to the adults' advantage to keep young on the territory in order to maximise their own reproductive success. If sibling aggression forced dispersal then it is unclear why the number of siblings did not affect dispersal timing; young with no siblings should not have dispersed early. An alternate hypothesis is that young were not dispersing, but rather were being killed, either on their natal territory or during a dispersal foray. If this is the case then it is unclear why dispersal patterns changed between years for the different sexes. To better understand why and when young disperse, observations need to focus on the period following the end of nutritional dependency. Further, the focus of study needs to be expanded into

the surrounding habitat in order to better understand the fate of individuals once they have left their natal territory.

Two of the main benefits commonly cited for cooperative breeding are that helpers decrease the amount of work done by the dominant pair and/or they increase the survival of offspring (for reviews see Hatchwell 1999 & Legge 2000). There is good evidence in my study that females benefit disproportionately compared with alpha males when beta males provide assistance. This situation persists despite the likelihood that when the beta males provide assistance, the alpha male might have lost paternity. Although subordinate male help during the fledgling period reduced the interval between breeding attempts it did not increase any measure of reproductive success and did not enhance female survival. Mine is the first study to show that the male and female benefit differently when a subordinate male provides assistance in feeding fledglings. Further, it provides a different picture of the effects of beta male help than did studies on this species which focussed solely on the nestling period.

Future studies on the effects of cooperative breeding during the fledgling period should focus on trying to obtain actual feeding rates of young after they have left the nest in order to allow direct comparisons of work rates between the fledgling and nestling periods.

The finding that adults may respond differently to beta male help during both the nestling and fledgling periods suggest that studies which focus only on nestlings may not provide a complete picture of the benefits and costs of cooperative breeding. Indeed, the focus on the nestling period in general provides an incomplete picture of avian reproductive success, considering that the fledgling period is often longer and more energetically expensive than the nestling period.

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